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INTÉRACTIONS MULTI-ÉCHELLES ENTRE RESSOURCES ABIOTIQUES, RÉSEAUX TROPHIQUES ET PROPRIÉTÉS DES ÉCOSYSTÈMES : NOUVEAUX JALONS THÉORIQUES POUR UNE ÉCOLOGIE INTÉGRATIVE

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INTERACTIONS MULTI-ECHELLES ENTRE RESSOURCES ABIOTIQUES, RESEAUX TROPHIQUES ET PROPRIETES DES ECOSYSTEMES

NOUVEAUX JALONS THEORIQUES POUR UNE ECOLOGIE INTEGRATIVE

Thèse présentée

dans le cadre du programme de Doctorat en Biologie

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PAR

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à Salomé Kraal

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RÉSUMÉ

Ce travail de thèse s'inscrit dans l'effort actuel de construction d'une écologie intégrative. J'y étudie les mécanismes d'interaction entre ressources abiotiques, réseaux trophiques et propriétés des écosystèmes, au moyen d'une expérience d'évolution, d'un modèle de méta-écosystème et d'un modèle bioénergétique d'assemblage d'écosystèmes. Les organismes modifient la disponibilité des ressources en les prélevant pour leur croissance. Inversement, la disponibilité des ressources influence la diversité et la composition en espèces du réseau trophique, en agissant comme force de sélection sur les traits d'acquisition des ressources (chap. 1, 5). Les propriétés de l'écosystème, telles que stabilité et productivité, dérivent des interactions entre la dynamique des ressources et celle du réseau trophique (chap. 2). Enfin, le fonctionnement de l'écosystème rétroagit sur les ressources abiotiques via le recyclage de la biomasse (chap. 2, 5). Ces processus interviennent lors de l'assemblage des réseaux trophiques et structurent le développement des écosystèmes (chap. 3-5). Dans cette thèse j'analyse ces mécanismes de rétroaction *biotique-abiotique* sur plusieurs échelles d'organisation, d'espace et de temps. Notamment, les modèles développés ici fournissent des outils novateurs pour étudier les mécanismes de construction des écosystèmes, en mettant en évidence les liens entre métabolisme des espèces, structure du réseau trophique et fonctionnement de l'écosystème, et leur variation au cours du temps. Ce travail ouvre de vastes perspectives de recherche en combinant les derniers progrès d'une écologie intégrative dans une conception mécaniste du développement des écosystèmes.

Mots-Clés **:** biodiversité, développement des écosystèmes, assemblage des communautés, méta-écosystèmes, recyclage, nutriments inorganiques, modèle bioénergétique

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ENGLISH TITLE

Multi-scale feedbacks between abiotic resources, food webs and ecosystem properties

New theoretical milestones for an integrative ecology

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ABSTRACT

This thesis participates to the current effort towards the construction of an integrative ecology. I study the feedback mechanisms between abiotic resources, food webs and ecosystem properties, through an evolution experiment, a model of metaecosystem, and a bioenergetic ecosystem assembly model. Organisms modify resource availability by consuming them for their growth. Conversely, resource availability influences the species diversity and composition of the food web, by acting as a selection pressure on traits for resource acquisition (chap. 1, 5). Ecosystem properties, such as stability and productivity, derive from the interactions between resource and food web dynamics (chap. 2). Finally, ecosystem functioning feeds back on abiotic resources through the recycling of biomass (chap. 2 and 5). These processes occur during the food web assembly and drive the development of ecosystems (chap. 3-5). In this thesis I analyze these *biotic-abiotic* feedback mechanisms on several scales of organization, space and time. The models developed here provide innovative tools to study the mechanisms of ecosystem construction by pointing out the links between species metabolism, food web structure and ecosystem functioning, and their variation through time. This work opens wide research perspectives, as it combines the most recent progress of an integrative ecology into a mechanistic framework of ecosystem development.

Keywords: biodiversity, ecosystem development, community assembly, metaecosystems, inorganic nutrients, recycling, bioenergetic model

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TABLE DES MATIÈRE

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

BEF	Biodiversité et Fonctionnement des Écosystèmes
(modèle) BEA	(modèle) Bioénergétique d'Assemblage d'Écosystème
chap.	chapitre (or chapter)
CNRS*	Centre National de la Recherche Scientifique
iDiv*	German Center for Integrative Biodiversity Research
IRD*	Institut de Recherche pour le Développement
INRA*	Institut National de la Recherche Agronomique
UM2*	Université Montpellier 2
UQAR*	Université du Québec à Rimouski

* *Acronymes utilisés dans les pages liminaires*

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INTRODUCTION GÉNÉRALE

Ce travail de thèse a pour objet général d'étudier les mécanismes par lesquels les espèces et les ressources inorganiques s'influencent réciproquement, à différentes échelles, au travers du fonctionnement des écosystèmes. Il participe d'un mouvement de fond de construction d'une écologie intégrative, qui vise à mieux comprendre le fonctionnement des systèmes naturels et leur réponse aux changements globaux. Cette écologie intégrative se développe dans plusieurs directions en regroupant les apports de disciplines ayant, jusqu'il y a peu, évolué séparément. Je propose ici de poser de nouveaux jalons théoriques dans cet effort d'intégration.

Dans cette introduction, Je présente d'abord le contexte très général dans lequel la thèse se place, en m'appuyant sur la figure 1. Cela me permet d'évoquer les motivations sous-jacentes derrière l'approche théorique, et de définir les entités et processus généraux qui sont au cœur de ce travail. Ensuite je brosse un portrait rapide des deux écoles de pensées qui ont longtemps structuré la recherche sur le fonctionnement des systèmes écologiques, selon des points de vue différents, à savoir l'écologie des écosystèmes et l'écologie des communautés. Je détaille ensuite les récents efforts d'intégration de ces écoles qui me servent de cadre et d'outils de travail. Enfin, je replace les projets constituant cette thèse dans le contexte plus précis décrit par la figure 6. J'explicite comment leurs objectifs s'articulent entre eux et s'inscrivent dans la construction de cette écologie intégrative.

CONTEXTE

Les activités humaines provoquent des changements globaux, *i.e.* à l'échelle de la planète, qui ont de multiples répercussions sur les écosystèmes naturels à l'échelle locale (figure 1; Vitousek *et al.* 1997, Tylianakis 2008). Les écosystèmes sont constitués de groupes d'espèces qui interagissent entre elles, dites 'communautés biotiques', et avec leur

environnement physique, dit 'abiotique' (figure 1, flèches 1 et 2). Je définis le fonctionnement des écosystèmes comme étant l'ensemble des processus de transformation de la matière issus de ces interactions *abiotique-biotique* au sein des écosystèmes : transformation de la matière inorganique en matière organique via la croissance des organismes (figure 1, flèches 1 à 4), et de matière organique en matière inorganique via le recyclage (figure1, flèche 5). Les propriétés des écosystèmes qui en découlent

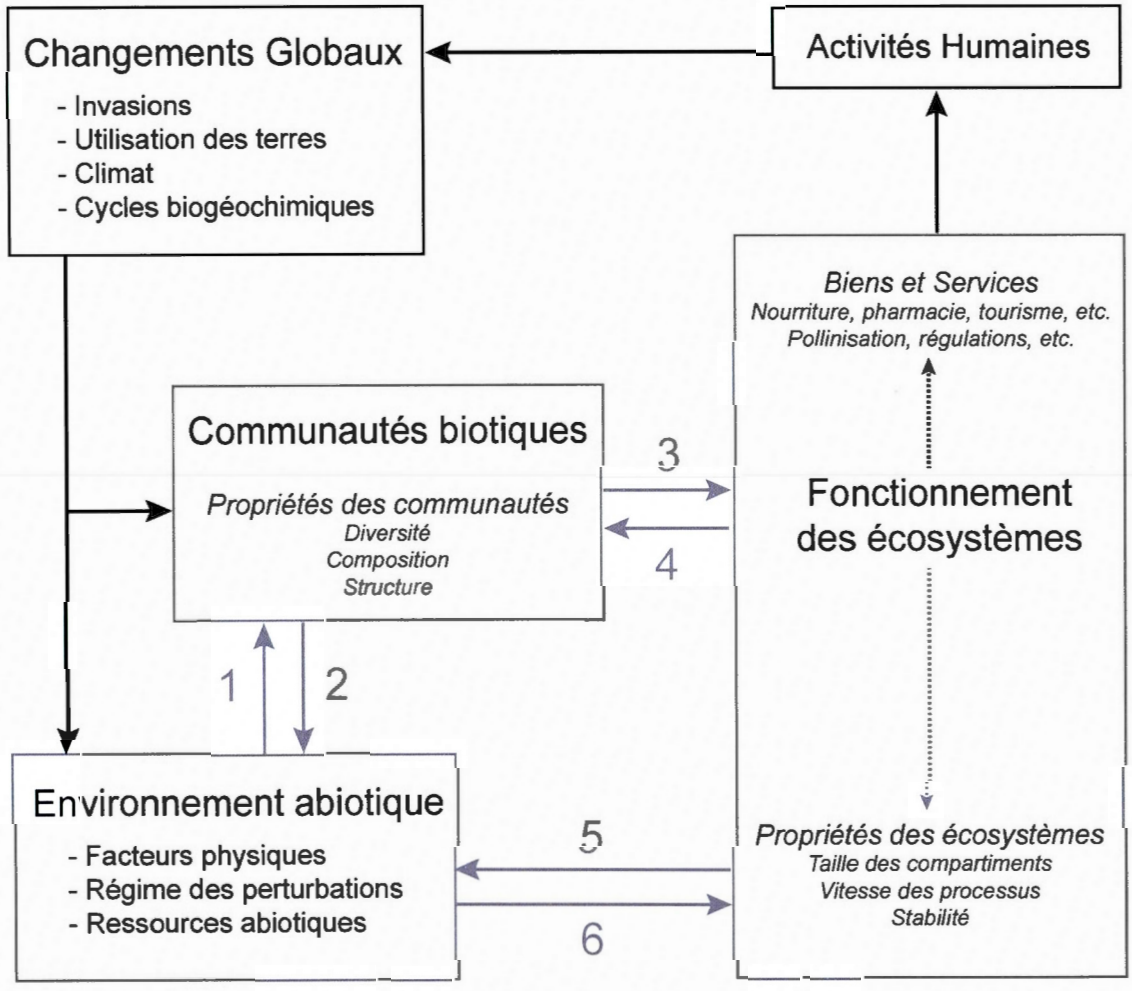

Figure 1 Interactions entre activités humaines et environnements abiotique et biotique

Modifiée d'après des figures issues de Hooper *et al.* 2005 et Chapin *et al.* 2000
Les flèches montrent l''effet sur' et non les flux de matière

comprennent : la tailles des principaux compartiments de l'écosystème (*i.e.* quantité de ressources inorganiques, de détritus et de biomasse; et à une échelle plus fine : abondances relatives des espèces), la vitesse des processus (production de biomasse par unité de temps, productivité, c'est-à-dire production de biomasse par unité de biomasse et de temps, vitesse de minéralisation, *etc.*) et leur stabilité (voir McCann 2000 pour les différentes métriques que cela recouvre).

Impacts directs et indirects des changements globaux sur les communautés

Les changements globaux peuvent affecter les communautés biotiques directement ou indirectement. Les impacts directs peuvent consister par exemple en une surexploitation des populations d'espèces d'intérêt commercial (exemple de la surpêche : Jackson *et al.* 2001, Mullon *et al.* 2005), ou en un déclenchement d'invasions biologiques (Lowry *et al.* 2012). Notamment, les activités humaines transportent des espèces hors de leur milieu d'origine, où leurs populations sont régulées, vers des écosystèmes qu'elles peuvent envahir en l'absence de prédateurs naturels (Mack *et al.* 2000). Surexploitation et invasions biologiques bouleversent les communautés en modifiant les abondances relatives des espèces et l'équilibre des interactions (Frank *et al.* 2005, White *et al.* 2006), menant potentiellement à des extinctions en cascade (Paine 1974, Estes *et al.* 1998).

Impacts indirects via des modifications de l'environnement abiotique

Les changements globaux peuvent aussi affecter les communautés biotiques indirectement, en détruisant les habitats des espèces ou en modifiant l'environnement abiotique (figure 1, flèche 1). L'exploitation des terres par les hommes accapare et fragmente les habitats naturels (Fahrig 2003), ce qui peut provoquer des extinctions retardées de populations (Tilman *et al.* 1994, Hanski et Ovaskainen 2002, Helm *et al.* 2006, Mouquet *et al.* 2011). D'autre part, les changements des paramètres physiques des habitats

et de la disponibilité des ressources inorganiques se généralisent (Millenium Ecosystem Assessment 2005).

Paramètres physiques

Les changements des paramètres physiques des habitats, comme la température ou le pH (Galloway 1995, Pörtner 2008), ont des conséquences indirectes à grande échelle sur les communautés biotiques. L'acidification des océans, due au réchauffement et à l'augmentation du CO_2 atmosphérique, affecte le développement des organismes à coquilles (Orr *et al.* 2005) et des récifs coralliens (Hoegh-Guldberg *et al.* 2007), ce qui est susceptible de déstabiliser profondément les communautés aquatiques. Le réchauffement climatique entraîne aussi des migrations vers les hautes latitudes d'espèces qui tentent de suivre leur optimum climatique (Devictor *et al.* 2008). Des extinctions surviennent aux limites des distributions pour les espèces les moins mobiles, ou à cause de barrières géographiques empêchant les migrations (Lasram *et al.* 2010). Enfin, un réchauffement peut modifier les interactions au sein des communautés biotiques parce que les espèces n'y répondent pas forcément de la même manière (Vucic-Pestic *et al.* 2011). Ainsi, des consommateurs peuvent être privés de ressource si les espèces dont ils se nourrissent ne se déplacent pas à la même vitesse qu'eux, ou si leurs phénologies se décalent de telle manière que la ressource n'est pas disponible au bon moment pour le consommateur (Winder et Schindler 2004, Edwards et Richardson 2004). Le changement du climat se traduit également par une plus grande variabilité, par exemple des précipitations, ou de l'occurrence d'évènements climatiques destructeurs. Cela impose aux espèces d'avoir des stratégies de croissance adaptées à ce contexte de variabilité pour pouvoir survivre (Stenseth *et al.* 2002, Lindner *et al.* 2010).

Ressources inorganiques

Enfin un des impacts anthropogéniques majeurs sur l'environnement est la modification des cycles biogéochimiques (Galloway et al. 2004, Magnani et al. 2007, Duce et al. 2008), par l'émission massive, entre autres, de gaz carbonique et d'oxydes d'azote dans l'atmosphère. Une déstabilisation des communautés biotiques peut s'ensuivre, par

exemple lorsque le phénomène de déposition atmosphérique enrichi les écosystèmes en azote (Carpenter *et al.* 1998), ou que les eaux usées ou des excédents de fertilisants agricoles sont lessivés vers les systèmes aquatiques (Camargo et Alonso 2006). Les enrichissements en azote ou en phosphore conduisent à un vaste phénomène d'eutrophisation des eaux côtières et des lacs, en causant une multiplication de cyanobactéries, de micro-algues ou de plantes flottantes à leur surface (Scheffer *et al.* 2003; figure 1, flèche 1). Dans les systèmes fermés comme les lacs peu profonds, cet état peut être difficilement réversible, même en retirant la source de pollution, car le déséquilibre de la structure des communautés biotiques rétroagit sur l'environnement abiotique (Scheffer et

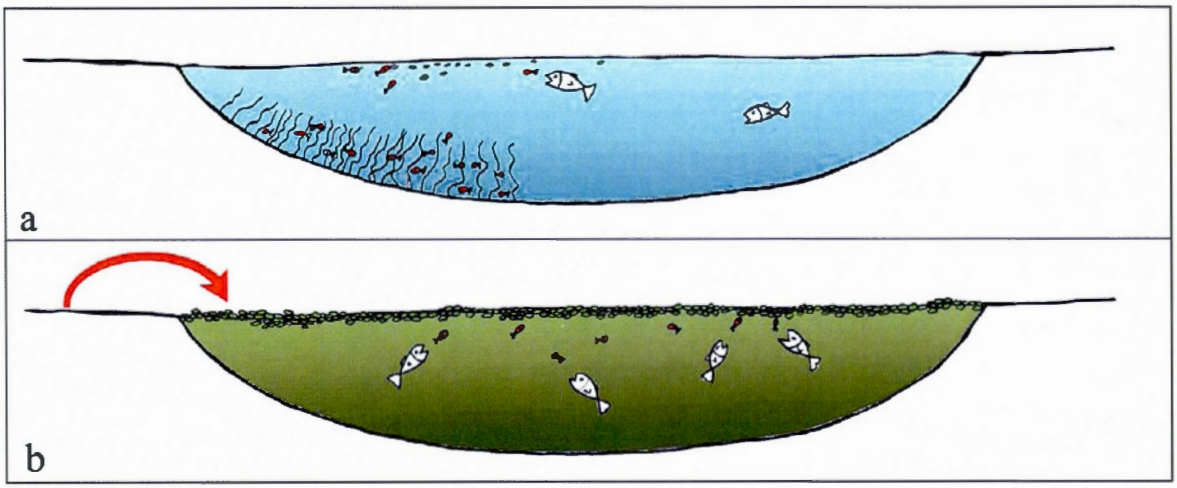

Figure 2 Eutrophisation d'un lac dû à un ajout de nutriments inorganiques

van Ness 2004; figure 1, flèche 2). Ainsi, un lac initialement oligotrophe, aux eaux gardées claires grâce au broutage des micro-algues par des poissons herbivores (figure 2a, poissons rouges), pourra basculer vers un stade eutrophe suite à un apport de nutriments (figure 2b, flèche rouge). Cet apport dope la croissance des micro-algues, tandis que la multiplication des poissons herbivores n'est pas assez rapide pour les empêcher de former un tapis. Privées de lumière, les macro-algues poussant sur les fonds des lacs meurent, et les poissons carnivores se multiplient aux dépens des populations d'herbivores laissées sans abris (figure 2b). Cela maintient les herbivores en sous-effectifs, les empêchant de

supprimer le tapis de micro-algues même si l'on retire l'apport en nutriments, empêchant du même coup le retour à un stade d'eaux claires (Scheffer 2009).

Interactions avec le fonctionnement des écosystèmes

Tous ces changements globaux affectent donc les propriétés des communautés biotiques, à savoir leur diversité en espèces (appelée richesse spécifique par la suite), leur composition (*i.e.* les identités des espèces, ou leurs traits caractéristiques), et leur structure (*i.e.* la topologie des liens d'interactions entre les espèces). Ces propriétés des communautés conditionnent le fonctionnement des écosystèmes (Hooper *et al.* 2005; figure 1, flèche 3). En effet, on a par exemple montré que plus les communautés sont diversifiées, plus grandes peuvent être leur production de biomasse (Hector *et al.* 1999, Tilman *et al.* 2001), ou leur résistance aux invasions biologiques (Kennedy *et al.* 2002; figure 1, flèche 3). Plus que la richesse en espèces à proprement parler, c'est la complémentarité fonctionnelle entre les espèces qui détermine la productivité des écosystèmes (Gross *et al.* 2007), et la redondance fonctionnelle (nombre d'espèces qui assurent une même fonction) qui prémunit contre la perte de fonctions écosystémiques suite à l'extinction d'espèces (Reich *et al.* 2012). L'environnement abiotique peut également directement influencer le fonctionnement des écosystèmes (figure 1, flèche 6). Par exemple une augmentation de la température stimule la production primaire (Brown *et al.* 2004), ce qui modifie la structure des communautés (figure 1, flèche 4), pouvant provoquer l'extinction de prédateurs (Petchey *et al.* 1999). Une augmentation de la température peut aussi stimuler la respiration microbienne (Kirschbaum 1995), et accélérer la minéralisation de la matière organique qui réapprovisionne l'écosystème en nutriments inorganiques (figure 1, flèche 5). Cette boucle d'interaction entre communauté biotique, fonctionnement de l'écosystème et environnement abiotique est bien illustrée, par exemple, avec l'invasion de certaines îles de Nouvelle-Zélande par des rats transportés par les hommes (Fukami *et al.* 2006). En comparant le fonctionnement de ces îles avec celui d'autres îles proches ayant des écosystèmes similaires, Tadashi Fukami et ses collègues (2006) ont trouvé que les rats, en

mangeant les oiseaux marins (plus précisément leurs œufs, déposés dans des trous creusés dans le sol), diminuent indirectement la respiration de la litière, la fertilité du sol, et la diversité de la plupart des organismes du sol. En l'absence de rats, les oiseaux enrichissent l'écosystème en déféquant sur place alors qu'ils se nourrissent en mer.

Retour sur les sociétés humaines

In fine, les changements dans le fonctionnement des écosystèmes se répercutent sur les biens et services qu'ils rendent à l'homme (Naeem *et al.* 2009, Cardinale *et al.* 2012). Cette terminologie de biens et de services écosystémiques a été créée pour attribuer une valeur aux écosystèmes, afin de construire un argumentaire économique à la nécessité de protéger les écosystèmes et la biodiversité (Balvanera *et al.* 2006). Les biens et services sont donc un équivalent anthropocentré des propriétés des écosystèmes (Hooper *et al.* 2005, Naem *et al.* 2009). Ils se réfèrent respectivement aux éléments des écosystèmes dont la valeur économique est directement quantifiable (*e.g.* nourriture, matériaux de construction, tourisme), et aux processus globaux qui bénéficient indirectement aux hommes (*e.g.* pollinisation, régulation de la composition atmosphérique). La rétroaction des activités humaines sur ce que leur apporte les écosystèmes est particulièrement criante avec l'exemple des écosystèmes marins. Ainsi, la surpêche, la pollution et la destruction des habitats marins font s'effondrer la biodiversité en poissons (-29% entre 1950 et 2003) et en invertébrés des océans, ce qui a pour effet, entre autres, de diminuer de 33% le nombre de pêcheries côtières viables à travers le monde (Worm *et al.* 2006).

Vers une écologie intégrative

Jusqu'il y a peu les composantes de la complexité des écosystèmes faisaient l'objet de champs de recherche relativement indépendants. L'écologie des écosystèmes s'est concentrée sur l'étude des flux d'énergie et de matière à travers les écosystèmes (boîtes 'environnement abiotique' et 'fonctionnement des écosystèmes', et flèches 5 et 6 de la

figure 1), en minimisant le rôle des interactions biotiques. L'écologie des communautés s'est concentrée, elle, sur les interactions entre espèces et la dynamique des populations (boîte 'communauté biotique' de la figure 1), en négligeant les possibles interactions réciproques avec l'environnement. Cette compartimentation issue de l'histoire de l'écologie a permis de poser des fondements théoriques, expérimentaux et empiriques solides pour ces différents aspects, mais ne permet pas de prendre en compte l'ensemble des rétroactions qui expliquent le fonctionnement des communautés biotiques ou/et des écosystèmes. Le rythme auquel surviennent les changements globaux catalyse l'étude de la relation entre biodiversité et fonctionnement des écosystèmes (Hooper *et al.* 2005, 2012, De Mazancourt *et al.* 2013, Loreau and De Mazancourt 2013), impliquant la construction d'une écologie plus intégrative permettant de comprendre ces rétroactions complexes (Naem *et al.* 2009, Loreau 2010a, 2010b). Ma thèse se situe dans cet effort d'élucidation des mécanismes d'interaction entre environnement abiotique, communautés biotiques et fonctionnement des écosystèmes (boîtes grises de la figure 1).

UNE ÉCOLOGIE COMPARTIMENTÉE

Écologie des écosystèmes

L'écologie des écosystèmes est centrée sur la caractérisation et la quantification des flux de matières et d'énergie entre monde vivant et environnement abiotique. Elle intègre les propriétés physico-chimiques des écosystèmes, et applique les principes de la thermodynamique au vivant pour comprendre les processus de transformation de la matière au sein des écosystèmes (Odum 1953, 1969). Le terme « écosystème » est introduit par Tansley en 1935 pour désigner une unité de base de la nature, qui comprend un environnement physique, dans lequel des espèces interagissent entre elles ainsi qu'avec l'environnement. La notion d'unité est suggestive. En général, les limites de l'écosystème sont définies par une intensité plus forte des interactions entre ses éléments, relativement à l'intensité des interactions avec l'extérieur. L'écologie des écosystèmes représente

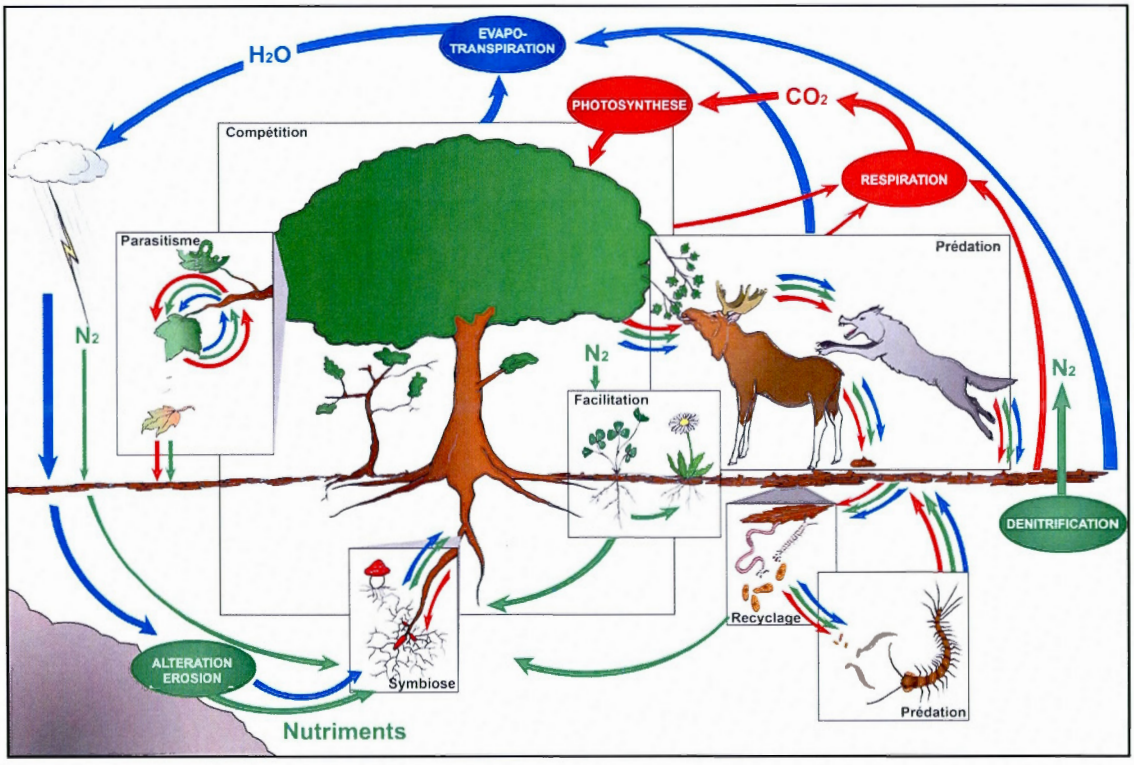

Figure 3 Interactions biotiques et processus de transformation biogéochimiques

typiquement les écosystèmes par de grands compartiments de stock de matière (inorganique ou organique) entre lesquels circulent des flux (figure 3, flèches). Elle regroupe les espèces selon les grands processus qui structurent le fonctionnement des écosystèmes : les producteurs primaires, qui produisent de la biomasse (*i.e.* matière organique) à partir de matière inorganique, les consommateurs primaires, qui se nourrissent des producteurs primaires, les consommateurs secondaires, qui se nourrissent des consommateurs primaires, les détritivores, qui consomment la matière organique morte, *etc.* Le détail des interactions entre individus ou espèces (boîtes de la figure 3) n'est pas pris en compte. L'écologie des écosystèmes construit une vision globale du fonctionnement des écosystèmes, en mettant l'accent sur les échanges avec l'environnement abiotique (figure 3, bulles de couleur) et les grands processus de circulation de la matière : l'altération et l'érosion des roches fournissent des nutriments inorganiques pour les producteurs primaires. Ceux-ci grâce à l'énergie solaire fixent du carbone atmosphérique par photosynthèse en produisant de la matière organique qui sert de nourriture de base pour les consommateurs. Les organismes produisent des détritus et meurent. Cette matière organique est recyclée (*i.e.* décomposée et minéralisée) en matière inorganique, rendue alors de nouveau disponible comme ressource pour les producteurs primaires. Par ailleurs, l'évapotranspiration, la respiration des organismes et la dénitrification par certaines bactéries rejettent respectivement de la vapeur d'eau, du dioxyde de carbone et de l'azote dans l'atmosphère. L'eau re-circule dans les écosystèmes par les précipitations, l'azote par la déposition atmosphérique et la fixation par les légumineuses (Houlton *et al.* 2008) et le carbone par la photosynthèse.

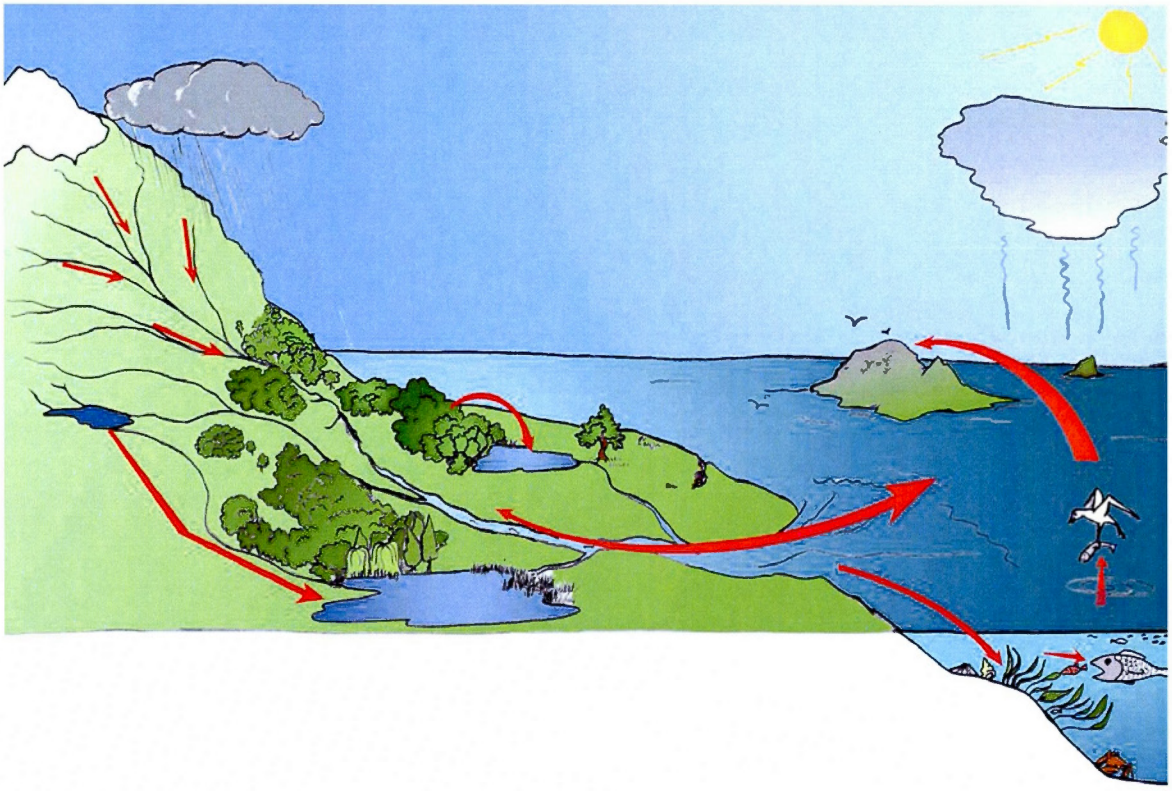

Figure 4 Transports de nutriments à l'échelle du paysage

Ces processus s'inscrivent à différentes échelles d'organisation. Ramon Margalef (1963) et Eugène Odum (1953, 1969) ont décrit comment ceux-ci interviennent dans le développement et la maturation des écosystèmes. Les cycles et transports de matière sont aussi considérés à une échelle plus large, définie par la structure physique du paysage (figure 4, flèche rouges, Turner 2005), comme par exemple à l'échelle d'un bassin versant (*e.g.* bassin hydrographique d'Hubbard brook : Whittaker *et al.* 1974, Likens *et al.* 1996). Enfin, le vivant est perçu comme un nœud de couplage entre les grands cycles biogéochimiques (Schimel 1995, Cotner et Biddanda 2002, Houlton *et al.* 2008). Ces cycles font aussi l'objet de quantification à l'échelle de la planète (*e.g.* le cycle de l'azote; Galloway *et al.* 2004).

Écologie des Communautés

L'écologie des communautés s'est focalisée pour sa part, à une échelle d'organisation plus fine, sur les interactions entre espèces (figure 3, les boîtes décrivent les différents types d'interaction), et sur les mécanismes de coexistence entre espèces permettant d'expliquer la biodiversité (Hutchinson 1959, 1961). Dans les modèles théoriques de communautés, l'environnement est intégré de façon implicite dans les processus démographiques des espèces, par exemple dans le paramètre de mortalité (pouvant inclure des causes climatiques), ou dans la densité-dépendance de la croissance des populations traduisant la finitude des ressources (voir Loreau 2010b pour une comparaison détaillée des modèles entre écologie des communautés et écologie des écosystèmes).

La compétition pour les ressources a longtemps été considérée comme le principal type d'interaction structurant les écosystèmes terrestres et expliquant le changement des communautés au long du processus de succession (Clements 1916, Huston et Smith 1987). La coexistence des espèces est expliquée entre autres par la différentiation de niches (MacArthur 1957, MacArthur et Levins 1967, Tilman 1977), c'est-à-dire que les espèces peuvent coexister si les besoins fondamentaux à leur survie sont différents (Gause 1934, Hardin 1960; voir Chase et Leibold 2003, pour une revue sur le concept de niche écologique). La théorie du ratio de ressources en particulier, stipule que la coexistence est limitée par le nombre de ressources disponibles localement (Tilman 1980, 1982, Miller *et al.* 2005). Sur une ressource unique, l'espèce qui gagne la compétition est celle qui est capable de survivre avec le plus bas niveau de ressource. Dans ce cadre précis, la coexistence de nombreuses espèces peut être est expliquée par l'hétérogénéité de la distribution spatiale des ressources et par la spécialisation des espèces pour des ressources différentes (Chase et Leibold 2003). Dans certains cas néanmoins, comme dans les milieux aquatiques où la répartition spatiale des ressources est relativement homogène, le nombre de ressources différentes paraît très petit par rapport à la grande biodiversité (« Paradox of the plankton » *sensu* Hutchinson 1961). D'autres sources de coexistence ont alors été avancées, comme avec la théorie des perturbations intermédiaires (Connell 1978, Sousa 1979, 1984, Petraitis *et al.* 1989, Molino et Sabatier 2001) qui propose qu'un niveau

intermédiaire de perturbations favorise la diversité, d'une part en empêchant les espèces les plus compétitives de s'accaparer les ressources et d'exclure les autres (comme ça peut-être le cas dans des milieux trop homogènes), d'autre part en n'imposant pas des conditions environnementales trop sévères qui permettraient à peu d'espèces de survivre. La coexistence est alors possible si les traits des espèces (*i.e.* leurs caractéristiques mesurables) témoignant de leur fonctionnement, présentent des compromis, par exemple tels que les plus compétitives soient les moins rapides à coloniser l'écosystème après une perturbation (« competition – colonization trade-off »; par exemple dans Bolker et Pacala 1999).

La prédation structure également la coexistence des espèces. De deux espèces-proies qui partagent le même prédateur, celle qui survit à long terme est celle qui peut supporter la plus grande population de prédateurs (situation de « compétition apparente »; Holt et Lawton 1994, Holt *et al.* 1994, 2001). La combinaison des interactions de compétition et de prédation peut mener à des effets indirects complexes (Wooton 1994, 2002, Chase *et al.* 2002, Poisot *et al.* 2013), qui dépendent de la structure du réseau d'interactions entre espèces. Une vaste littérature s'est développée pour décrire les réseaux « trophiques » (se référant strictement aux liens de consommation entre espèces), leurs propriétés structurelles et dynamiques (Polis et Strong 1996, Dunne 2006, De Ruiter *et al.* 2005). Des modèles simples ont été développé, dont l'un des plus populaires est le modèle de niche (Williams et Martinez 2000), pour reproduire des structures réalistes de réseaux trophiques en partant de l'hypothèse que l'on en connaît la diversité et la connectance (proportion des interactions réelles entre les espèces du réseau sur l'ensemble des interactions possibles théoriquement). Des investigations plus poussées ont par la suite exploré, par exemple, la signification écologique de la fréquence de certains modules dans la structure de ces réseaux (Stouffer 2010), ou la stabilité des réseaux face à des perturbations (Montoya *et al.* 2006, 2009). Les communautés biotiques peuvent aussi être fortement structurées par d'autres types d'interactions (figure 3, voir les boîtes), comme la symbiose (Van der Heijden *et al.* 1998) ou la facilitation (Bonanomi *et al.* 2011). L'écologie des communautés commence tout juste à intégrer interactions consommateur-ressource et interactions mutualistes (Kéfi *et al.*

2012). Ce travail de thèse se concentre cependant sur les interactions trophiques, comme précisé plus loin.

DÉVELOPPEMENT D'UNE ÉCOLOGIE INTÉGRATIVE

L'écologie des écosystèmes et l'écologie des communautés ont développé les fondements de nos connaissance sur les systèmes naturels. Cependant les dernières avancées, par exemple en écologie spatiale (Gravel *et al.* 2010a et 2010b, Massol *et al.* 2011), mettent en évidence des propriétés émergentes des écosystèmes lorsque différentes échelles d'organisation, d'espace et/ou de temps sont considérées.

Dans cette section, je présente rapidement les nouveaux axes de recherches qui intègrent ces différentes échelles et créent des ponts entre écologie des écosystèmes et écologie des communautés. J'expose d'abord les progrès d'intégration entre les différentes échelles d'organisation, depuis les traits des espèces jusqu'au fonctionnement de l'écosystème. Puis j'expose quels outils et cadres conceptuels ont été développés pour prendre en compte les échelles spatiales et temporelles de la construction et du fonctionnement des communautés, et par extension des écosystèmes. Je focalise naturellement sur les outils que j'ai utilisés dans cette thèse.

Intégration des échelles d'organisation

L'incorporation d'éléments de physiologie des organismes au sein des interactions écologiques a accompli une étape décisive dans l'intégration des différentes échelles d'organisation depuis les organismes jusqu'au fonctionnement des écosystèmes, et même à une échelle plus globale. Cette avancée est au cœur, principalement, de deux nouveaux champs de recherche, l'écologie stœchiométrique (Elser *et al.* 1996, Sterner et Elser 2002, Moe et al. 2005, Elser 2006, Elser et Hamilton 2007) et la théorie métabolique de l'écologie (Brown *et al.* 2004). La première prend en compte les contraintes physiologiques des organismes liées aux disponibilités relatives des différents nutriments inorganiques

essentiels à leur croissance. La seconde envisage les flux de matière et d'énergie au sein des écosystèmes à travers le métabolisme des organismes.

Écologie stœchiométrique

Richter définissait en 1792 la stœchiométrie comme étant « la science qui mesure les proportions quantitatives ou rapports de masse dans lesquels les éléments chimiques sont impliqués ». L'écologie stoechiométrique s'intéresse, d'une façon large, au passage des molécules au travers du vivant. Le titre évocateur de son livre fondateur est évocateur : « La biologie des éléments des molécules à la biosphère », porte sans détours une perspective d'intégration des différents échelles de transformation de la matière (Sterner et Elser 2002). En cela, cette approche est héritière de l'écologie des écosystèmes. Dans cette perspective, les organismes vivants représentent un des principaux nœuds de couplage des cycles biogéochimiques, par le biais du recyclage et de leurs contraintes physiologiques (Elser 2006). Pour leur survie, les organismes doivent assurer les fonctions biologiques essentielles que sont l'acquisition des ressources, la biosynthèse (multiplication des cellules), la structure (croissance des cellules) et la défense (*e.g.* contre les prédateurs). Ces fonctions biologiques font appel à différentes molécules qui correspondent à des besoins différents en éléments chimiques (Sterner et Elser 2002). Par exemple, la fonction de biosynthèse implique la production d'une grande quantité d'acides nucléiques pour la réplication et la transcription de l'ADN, et notamment d'ARN ribosomial pour la synthèse des protéines. Ces molécules sont particulièrement riches en azote et surtout en phosphore comparé aux autres molécules organiques. Des études ont alors montré que les organismes qui croissent plus vite que les autres sont composés d'une plus grande proportion de phosphore (« Growth Rate Hypothesis »; Elser *et al.* 2000, 2003, Makino *et al.* 2003, Kyle *et al.* 2006). La prise en compte des contraintes stœchiométriques des organismes permet d'affiner l'étude de la dynamique des populations (Andersen *et al.* 2004, Moe *et al.* 2005) et dévoile un niveau supplémentaire de complexité dans les interactions entre espèces et les conditions de leur coexistence (Loladze *et al.* 2000, Daufresne et Loreau 2001). Ainsi, la

physiologie des organismes détermine la circulation des nutriments au sein des écosystèmes au travers de l'acquisition des différents éléments chimiques essentiels à leur fonctionnement (Sterner et Elser 2002, Vrede *et al.* 2004).

Théorie métabolique de l'écologie

La théorie métabolique de l'écologie s'appuie sur des relations allométriques empiriques entre la masse corporelle des espèces, leurs taux biologiques (respiration, développement *etc.*) et la température, pour expliquer le fonctionnement des écosystèmes (*e.g.* production de biomasse) à travers le métabolisme des espèces (Brown *et al.* 2004, Price *et al.* 2012, Humphries et McCann 2014). Globalement, les organismes de taille ou de masse corporelle plus petite ont un métabolisme plus rapide que les gros organismes, ce qui entraîne des taux de croissance plus rapides et une productivité plus grande à l'échelle de la population. De plus, la vitesse des réactions chimiques augmentant avec la température, les flux bioénergétiques (*i.e.* de matière et d'énergie) sont aussi plus rapides quand la température augmente.

Yodvis et Innes ont incorporé ces contraintes bioénergétiques dans un modèle consommateur-ressource (1992). Par la suite, l'établissement d'une relation empirique entre la taille des proies et la taille de leurs prédateurs pour des écosystèmes variés (Brose *et al.* 2005, 2006a) a permis de développer des modèles de réseaux trophiques bioénergétiques (Brose *et al.* 2006b, Brose 2008, Berlow *et al.* 2009). Leur intérêt est multiple. En premier lieu, les allométries des taux biologiques avec la taille ou la masse corporelle des espèces permettent de réduire le nombre de paramètres des modèles, et de les paramétrer avec un trait relativement facile à mesurer sur tout type d'organisme. Ensuite, la prise en compte du métabolisme permet de passer aisément d'une échelle d'organisation à l'autre (organisme, population, communauté, écosystème) en caractérisant les taux de transfert de matière et d'énergie selon l'échelle (Woodward *et al.* 2005). Enfin, l'incorporation de la dépendance du métabolisme à la température (Vasseur et McCann 2005) donne un outil pour simuler et

comprendre la réponse des réseaux trophiques au réchauffement climatique (Petchey *et al.* 2010, Brose *et al.* 2012, Amarasekare et Coutinho 2014).

Intégration des échelles spatiotemporelles

La prise en compte des échelles spatiales a permis de mieux comprendre comment la diversité, la structure des communautés et le fonctionnement des écosystèmes au niveau local dépendent de leurs échanges avec la région environnante. Dans cette section j'expose d'abord l'exemple emblématique du débat sur la relation diversité-fonctionnement des écosystèmes, pour lequel la prise en compte de l'échelle spatiale s'est révélée déterminante dans l'interprétation des observations. Ensuite je présente deux champs particuliers de l'écologie, d'essor récent, centrés sur l'intégration de la composante spatiale. Leurs deux angles d'approche sont très différents : d'une part, ce que j'appellerais *l'écologie des paysages fragmentés* (les « méta – X ») considère différentes localités reliées par des flux spatiaux d'organismes ou de matières, et compare la coexistence des espèces aux niveaux régional et local. D'autre part *l'assemblage des communautés* se focalise sur une localité et considère l'arrivée dans cette localité d'organismes venant de la région environnante.

Relation Biodiversité – Fonctionnement des écosystèmes

L'étude de la relation entre biodiversité et fonctionnement des écosystèmes (BEF) est un bon exemple de la nécessité d'intégrer les différentes échelles spatiales pour comprendre les observations empiriques. Les recherches dans ce domaine ont d'abord suivi les deux démarches distinctes issues de l'écologie des écosystèmes et de l'écologie des communautés (Hooper *et al.* 2005). Les écologues des écosystèmes ont trouvé que la diversité variait avec la productivité d'un écosystème, selon une relation unimodale (Huston et DeAngelis 1994, Waide *et al.* 1999, Grime 2001; figure 5, points rouges). Jusqu'à un certain point, une fertilité croissante favorise la diversité en diminuant la compétition pour les nutriments ; à partir d'un certain seuil, la structure de l'habitat

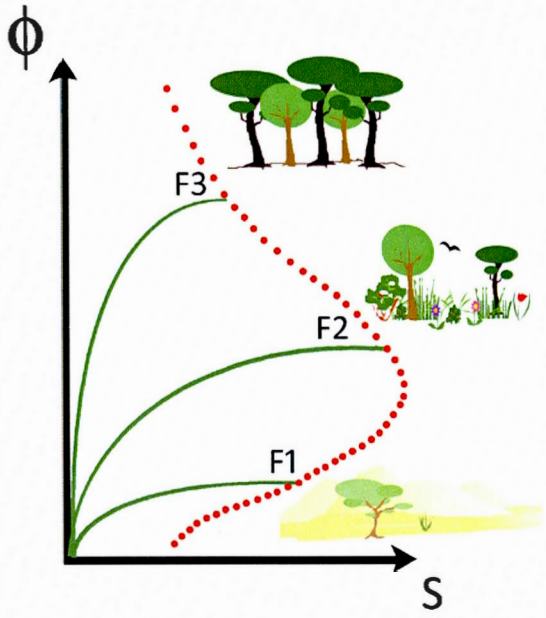

Figure 5 Intégration spatiale de la relation BEF

D'après une figure issue de Loreau *et al.* 2001

s'homogénéise, donc le nombre de niches et la diversité diminuent (Grime 1973). Les écologues des communautés ont trouvé une relation croissante (Hector *et al.* 1999, Tilman *et al.* 1997a, 2001; figure 5, lignes vertes) entre la diversité et le fonctionnement des écosystèmes, notamment la productivité. Cette relation est expliquée par deux mécanismes (Loreau *et al.* 2001, Hooper *et al.* 2005) : d'une part une communauté plus diverse a une plus grande probabilité de contenir une espèce très productive (effet de sélection) ; d'autre part elle utilise mieux les ressources disponibles si les espèces qui la composent sont spécialisées sur des niches différentes, induisant une plus grande production (effet de complémentarité; Tilman *et al.* 1997b, Loreau 1998c, Loreau *et al.* 2001).

Les approches *écosystèmes* et *communautés* se sont opposées dans la littérature à la fin des années 1990 (Huston 1997, Grime 1997, Schmid 2002). Cette apparente opposition des relations BEF trouvées par les deux écoles était due en fait à une mésentente sur l'échelle spatiale et la variable indicatrice du fonctionnement des écosystèmes considérées (Loreau *et al.* 2001; figure 5). Les écologues des communautés se sont placés à une petite

échelle, où la fertilité est homogène. Ils ont manipulé la diversité et observé la productivité *réalisée*. Au contraire, les écologues des écosystèmes ont suivi une variation de la fertilité (c'est-à-dire de la productivité *potentielle*) qui les a placé à une échelle plus large, où les variations de l'environnement influencent la diversité (figure 5).

Structure spatiale : Écologie d'un paysage fragmenté

La fragmentation du paysage induite par les activités humaines réduit la surface des habitats favorables à la survie des espèces et leur connectivité (Farhig 2003, Foley *et al.* 2005). Cela peut provoquer des extinctions retardées dues au temps de réponse de la dynamique des populations à la destruction de l'habitat (« extinction debt »; Tilman *et al.* 1994, Hanski et Ovaskainen 2002, Helm *et al.* 2006, Mouquet *et al.* 2011). Le morcèlement des habitats a impulsé des recherches pour comprendre son effet sur la dynamique des espèces. Les écologues ont développé des modèles considérant plusieurs sites reliés par des flux de dispersion, pour étudier la dynamique des espèces à l'échelle régionale. Ces modèles ont montré que des extinctions de populations au niveau local pouvaient être compensées par des flux de migration à l'échelle régionale (Levins 1969, Hanski 1991, 1998). L'étude de ces dynamiques d'extinction – colonisation trouvée pour des méta-populations (populations interconnectées), a été étendue à l'échelle des communautés avec le concept de méta-communautés (Leibold *et al.* 2004). La théorie des méta-communautés a formulé quatre paradigmes permettant d'expliquer différents mécanismes de coexistence à l'échelle d'une région. Ceux-ci impliquent soit de l'hétérogénéité environnementale entre sites qui permet à des espèces ayant des niches différentes de coexister régionalement en étant dominantes dans des sites différents (« species sorting »), et qui peut empêcher des extinctions locales par de la dispersion depuis des sites favorables (« mass effect »); soit les sites sont équivalents mais la dispersion des espèces est limitée, et la coexistence régionale découle d'une dynamique d'extinctions et de colonisations, les espèces pouvant être plus ou moins compétitives ou /et bonne colonisatrices (« patch dynamics »); soit les espèces sont équivalentes dans leurs capacités de compétition et de colonisation et la diversité régionale dérive de la balance entre les probabilités de gain d'espèces par immigration et spéciation et

de perte d'espèces par extinction et émigration (« neutral paradigm ») (voir Amaresakare *et al.* 2004, Leibold *et al.* 2004, Holyoak *et al.* 2005 pour plus de détails).

Le concept de méta-écosystème a été défini en parallèle (Loreau *et al.* 2003) pour ajouter les flux spatiaux de nutriments et de détritus à la compréhension des mécanismes de coexistence (Gravel *et al.* 2010a, 2010b). Ces flux de matière sont connus pour constituer une grande part des ressources dans de nombreux écosystèmes (Polis et Hurd 1996, Polis *et al.* 1997, 2004). Les méta-écosystèmes permettent de prendre en compte leur impact sur la dynamique communautés, mais aussi la rétroaction que la croissance des espèces exerce sur la disponibilité des ressources, en intégrant le recyclage local de la biomasse (Loreau 2010a, 2010b, Massol *et al.* 2011). Ce cadre conceptuel fournit ainsi un outil de synthèse des perspectives de l'écologie des communautés et de l'écologie des écosystèmes, mais il est cependant encore peu utilisé.

Assemblage des communautés

La théorie de l'assemblage des communautés s'est développée pour trouver des explications aux variations de diversité observées entre localités proches et d'environnement apparemment similaire (Samuels et Drake 1997, Belya et Lancaster 1999, Schröder *et al.* 2005, Chase 2003a, 2010). Dans cette perspective, on ne considère plus seulement les éléments présents dans une localité donnée, mais aussi toutes les espèces venant d'un ensemble plus large (*pool régional*) qui peuvent potentiellement coloniser cette localité. La plupart des études sur l'assemblage se sont attelées à déterminer à quel point la diversité des communautés est structurée par l'ordre dans lequel arrivent les espèces (séquence d'assemblage). Des expériences en nature ou en microcosme ont montré que cet ordre d'arrivée peut engendrer des effets de priorité, où les espèces arrivées en premier modifient les chances de succès des futurs colonisateurs (Alford et Wilbur 1985, Almany 2003). La trajectoire d'assemblage (*i.e.* la succession d'états pris par la communauté) diverge alors vers des communautés qui seront composées de différentes espèces lorsqu'elles atteignent un état stationnaire (Drake 1991, Jenkins et Buikema 1998, Fukami

et Morin 2003, Fukami *et al.* 2005, Chase 2003a). Par exemple Körner et ses collègues (2008) montrent que selon l'ordre dans lequel des plantes, ayant différentes fonctions dans l'écosystème, s'installent dans une parcelle, les compositions finales et les biomasses associées seront radicalement différentes. Les expériences ont l'avantage de tester ces hypothèses sur des organismes vivants, intégrant une variabilité plus réaliste des conditions environnementales (Drake 1991, Drake *et al.* 1993), mais elles ont l'inconvénient d'être souvent limitées dans le temps, ce qui ne certifie pas que les différences observées ne soient pas transitoires (Carpenter 1996). De plus elles ne permettent souvent pas aux espèces de retenter leur chance lorsqu'elles ont été exclues une première fois, alors que les conditions biotiques variant au cours de l'assemblage, pourraient leur permettre de s'installer plus tard. Ces limitations ont été résolues dans le travail théorique mené en parallèle (Morton *et al.* 1996, Law et Morton 1996, Lockwood *et al.* 1997, Fukami 2005). Les modèles d'assemblage construisent des communautés à partir de l'invasion séquentielle d'espèces venant d'un pool régional. Les évènements de colonisation se poursuivent jusqu'à ce que la composition de la communauté se stabilise. Ces avancées théoriques ont avéré que des communautés alternatives puissent exister malgré des conditions environnementales et des pools identiques d'espèces (Morton *et al.* 1996, Law & Morton 1996, Lockwood *et al.* 1997). Le développement de la théorie sur l'assemblage des communautés a surtout permis de décrire les facteurs qui accentuent ces impacts des contingences historiques sur les communautés (Chase 2003b), comme une plus grande diversité régionale (Law et Morton 1996, Fukami 2004), une plus grande productivité locale (Chase 2010), un environnement moins stressant (Chase 2007) ou une plus grande similarité des espèces (Peay *et al.* 2012). Cependant il n'existe pas de théorie générale sur les mécanismes à l'œuvre lors du processus d'assemblage, et le lien avec le fonctionnement et le développement des écosystèmes est encore peu évoqué.

NOUVEAUX JALONS THÉORIQUES

Problématique

D'importantes avancées ont été faites, d'une part pour expliquer les liens entre les différentes échelles d'organisation des systèmes écologiques, en incorporant les traits physiologiques des espèces (écologie stœchiométrique, théorie métabolique de l'écologie), d'autre part pour intégrer les échelles spatiales et temporelles dans l'étude des communautés. Ces progrès améliorent notre compréhension des écosystèmes en prenant en compte de nouvelles dimensions de leur complexité. Cependant, les interactions réciproques liant communautés biotiques et environnement abiotique au sein des écosystèmes sont encore peu intégrées simultanément.

L'objet de la thèse est de caractériser de nouveaux mécanismes d'interactions entre ressources abiotiques, réseaux trophiques et propriétés des écosystèmes. Je propose de poursuivre l'intégration de l'écologie des communautés et de l'écologie des écosystèmes en combinant les progrès évoqués précédemment, de manière à mieux caractériser les liens entre coexistence des espèces et flux de matière au sein des écosystèmes. Je développe des approches théoriques selon une échelle croissante de complexité, pour analyser plus particulièrement les interactions réciproques entre : (1) ressources inorganiques et stratégies de croissance des espèces (chapitre 1); (2) dynamique de la ressource et dynamique des espèces, dans un cadre spatialisé (chapitre 2); (3) dynamique d'assemblage des réseaux trophiques et fonctionnement des écosystèmes (chapitres 3 à 5).

Cadre de la thèse

Pour préciser le cadre de la thèse je reprends les composantes générales de la figure 1 et je les redéfinis dans la figure 6 en fonction des problématiques développées dans mes cinq chapitres. Je souligne deux points en préliminaire à la présentation des chapitres.

Premier point, dans cette thèse je me focalise sur les flux de matière au sein des écosystèmes. Cela implique d'une part que je considère essentiellement les ressources

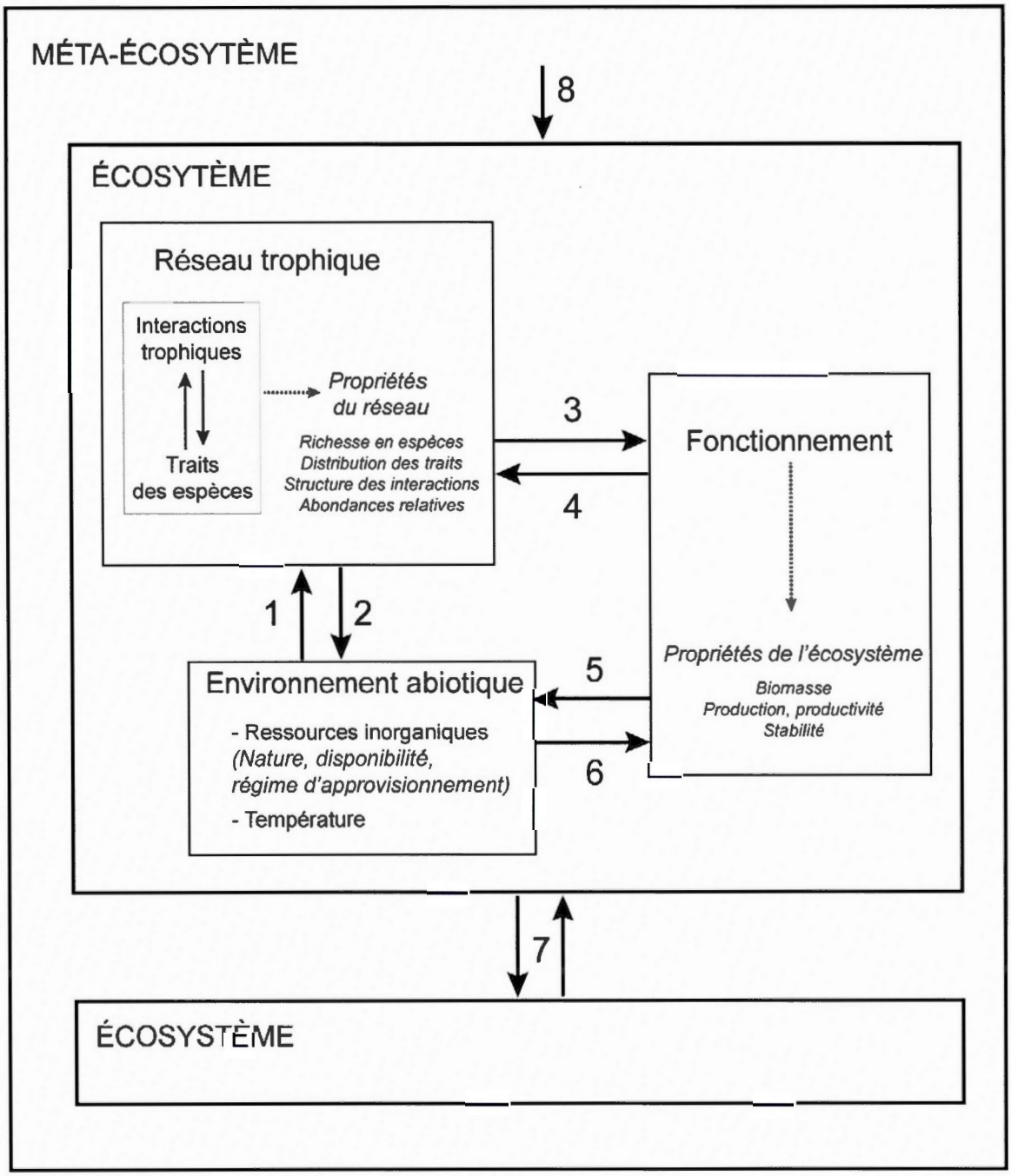

Figure 6 Interactions abiotique – biotique au sein des écosystèmes et au niveau régional

inorganiques comme composante de l'environnement abiotique. Je m'intéresse, selon les chapitres, à la nature de ces ressources inorganiques (éléments chimiques), à leur

disponibilité intrinsèque (fertilité de l'écosystème) et à leur dynamique (consommation par les organismes, recyclage, transports entre écosystèmes). D'autre part, pour ce qui est de la composante biotique, je me focalise sur les réseaux trophiques. Je m'intéresse uniquement aux traits des espèces liés à l'acquisition des ressources ou à leur métabolisme, et je ne prends en compte que les interactions trophiques. Par interactions trophiques, j'entends compétition et prédation. Ainsi, je n'intègre pas d'interactions hôte-parasite, ni d'interactions mutualistes autre que celles émergeant d'interactions indirectes au sein des réseaux trophiques. Les propriétés de fonctionnement des écosystèmes prises en compte sont donc liées aux processus de flux de matière. Ce sont les stocks (nutriments inorganiques ou biomasse), la vitesse des flux (production de biomasse par unité de temps, productivité, c'est-à-dire turn-over de la biomasse), mais aussi leur stabilité (précisé plus tard).

Second point, je considère la dimension spatiale du fonctionnement des écosystèmes de deux façons. Un écosystème est défini par son unité de fonctionnement, mais il n'est pas isolé. Les écosystèmes sont environnés d'autres écosystèmes avec lesquels ils échangent des organismes et des flux de détritus ou de matière inorganique (Polis *et al.* 1997, Loreau *et al.* 2003, Massol *et al.* 2011). Je tiens compte de ces échanges soit en représentant la structure spatiale, c'est-à-dire en explicitant les différents écosystèmes et les flux de dispersion qui les lient (figure 6, flèches 7), soit en me concentrant sur un écosystème qui reçoit des organismes venant d'une région environnante considérée implicitement (figure 6, flèches 8). Dans le premier cas j'utilise le cadre conceptuel des méta-écosystèmes (Loreau *et al.* 2003), qui permet d'étudier les interactions spatiales entre dynamiques des ressources inorganiques et dynamique des espèces (chapitre 2). Dans le second cas je m'inscris dans le cadre de l'assemblage des communautés et plus largement dans le cadre du développement des écosystèmes (distinction expliquée plus loin; chapitres 3 à 5). Cette perspective me permet d'étudier les mécanismes de construction d'un écosystème, à partir de la dispersion régionale des espèces.

Articulation des chapitres

Les chapitres de la thèse s'articulent suivant une échelle croissante d'organisation. Le premier chapitre traite des relations entre ressources inorganiques et espèces (figure 6 flèches 1 et 2) à l'échelle de la population, et se focalise sur un grain fin, celui des traits des espèces. Il traite plus précisément des liens entre leurs traits de croissance et d'acquisition des ressources.

Le second chapitre se situe à l'échelle de l'interaction entre deux populations. J'y étudie l'aspect dynamique de l'interaction entre croissance des populations et variation de la disponibilité en ressource inorganique, en intégrant la dynamique du recyclage (figure 6, flèches 1, 3, 5). J'analyse comment cette interaction fonctionne dans le cadre spatialisé des méta-écosystèmes (figure 6, flèches 7).

Les chapitres 3 à 5 examinent l'interaction ressource – espèces pour des réseaux plus complexes d'espèces. Ils visent à comprendre comment cette interaction structure la construction des écosystèmes. Pour cela, j'utilise le cadre défini par l'assemblage des communautés (figure 6, flèche 8). Avec le chapitre 3, je commence par étudier comment le processus d'assemblage structure la distribution des traits des espèces (ceux liés à la circulation des flux de matière, notamment masse corporelle et efficacité) dans le réseau trophique (figure 6, flèche 8 et flèches entre traits des espèces et interactions trophiques), et comment cette distribution des traits dépend de la température (figure 6, flèches 6 et 4). Ensuite dans le chapitre 4 je teste comment les caractéristiques du processus d'assemblage (timing d'arrivée des espèces) peuvent modifier la distribution de ces traits, et par là affecter la diversité du réseau trophique et le fonctionnement de l'écosystème (figure 6, flèches 3, 4 et 8). Enfin, dans le chapitre 5, je complète mon intégration ressources inorganiques-espèces-fonctionnement de l'écosystème en incorporant le recyclage de la matière organique dans la dynamique d'assemblage (figure 6, flèches 5 et 1). Cela me permet d'expliciter les interactions réciproques entre diversité et fonctionnement dans le cadre du développement des écosystèmes.

Je présente ci-dessous l'objet et les motivations des projets constituant les différents chapitres. J'évoque rapidement le principe général de la méthode utilisée.

Chapitre 1 – Interactions entre ressources inorganiques et stratégie de croissance des espèces

A la base de l'interaction entre ressources inorganiques et réseaux trophiques, il y a le besoin des espèces en ressources spécifiques pour assurer leurs fonctions vitales, dont croissance et leur capacité à acquérir ces ressources. D'une part l'écologie stœchiométrique a montré un lien entre la stœchiométrie des organismes et leur taux de croissance (Sterner et Elser 2002). D'autre part la coexistence des espèces implique souvent des compromis entre leurs traits d'histoire de vie (Mueller et Ayala 1981, Kneitel et Chase 2004, Edwards *et al.* 2011, 2013), notamment entre leur capacité à croître vite et leur compétitivité pour l'acquisition des ressources (Edwards *et al.* 2013), ou entre leurs capacités d'acquisition pour différentes ressources (Edwards *et al.* 2011). Ces compromis entre traits définissent ce que j'appellerais une stratégie de croissance : c'est la combinaison des traits impliqués dans la croissance, qui témoigne d'une hiérarchie particulière entre les grandes fonctions physiologiques de l'organisme (biosynthèse, acquisition des ressources, structure, défense). Le cadre de l'écologie stœchiométrique permet d'envisager ces stratégies de croissance selon leur demande caractéristique en éléments chimiques, correspondant à la composition des molécules des fonctions physiologiques privilégiées. Les contraintes physiologiques des organismes peuvent fournir une explication mécaniste à la relation entre des traits démographiques tel que le taux de croissance et leur compétitivité pour les ressources. Par exemple des organismes ayant un plus fort taux de croissance *per capita* devraient être plus contraints par des limitations en phosphore, dont ils ont besoin pour leur forte production en acides nucléiques. Ainsi, la disponibilité des ressources inorganiques devrait favoriser certaines stratégies plutôt que d'autres (et en retour la compétitivité des espèces pour les ressources devrait moduler la disponibilité des ressources).

Dans ce chapitre j'étudie le lien entre capacité de croissance et la compétitivité pour les ressources en milieu contrôlé, en faisant émerger des stratégies de croissance à partir d'une population unique de bactéries, lors d'une expérience d'évolution. L'objectif est

d'éliminer le plus de sources de variation pour déterminer l'implication de la physiologie de la cellule dans cette relation.

Chapitre 2 – Interactions spatiales entre ressources inorganiques et dynamique plante-herbivore

Un effet bien connu de la disponibilité des ressources sur les espèces est décrit par le « paradoxe de l'enrichissement » (Rosenzweig 1971) : dans une interaction trophique entre une proie et son prédateur, si la ressource de la proie augmente, cela peut, au contraire de bénéficier à l'abondance des espèces, déstabiliser leur dynamiques (*i.e.* provoquer des fluctuations), et éventuellement conduire à leur extinction successive. Ce phénomène a été essentiellement étudié selon le prisme de l'écologie des communautés, c'est-à-dire avec une considération implicite de l'environnement dans les paramètres des espèces, et en se focalisant uniquement sur l'interaction entre les espèces (*e.g.* Jansen 1995). Étant donné que l'accroissement de la ressource est la cause de la déstabilisation, il paraît intéressant d'inclure la dynamique de la ressource inorganique de façon explicite. DeAngelis a exploré la stabilité de dynamiques plante-herbivore en présence de recyclage et pour différents niveaux de fertilité à une échelle locale (1980, 1992). Cependant, la structure spatiale est connue comme un facteur important de régulation empêchant la déstabilisation par enrichissement dans le cadre des méta-communautés (Hauzy *et al.* 2013). De plus les transports de nutriments et de détritus entre écosystèmes peuvent fournir une importante partie des ressources d'un écosystème (Polis *et al.* 1997, 2004). Il paraît donc essentiel d'inclure structure spatiale et dynamique explicite des nutriments pour comprendre la stabilité des interactions consommateur-ressource.

Dans ce second chapitre je propose d'étudier comment les dynamiques locales et spatiales des ressources et des espèces interagissent et déterminent la stabilité régionale, conjointement avec la fertilité de l'écosystème. Pour ce faire, je revisite le paradoxe de l'enrichissement dans le cadre des méta-écosystèmes. J'utilise un modèle simple couplant par des flux spatiaux deux écosystèmes habités par les populations d'une espèce de plante

et d'un herbivore, dont la biomasse est recyclée localement (modèle d'après Gravel *et al.* 2010a).

Chapitres 3 à 5 : Modèle d'assemblage d'écosystème

Dans les trois chapitres suivants, j'utilise un modèle bioénergétique d'assemblage d'écosystème (BEA), dans lequel les ressources inorganiques sont explicitement représentées, pour étudier les mécanismes de construction des réseaux trophiques et le développement des écosystèmes. Les espèces provenant de la région environnante arrivent et tentent de s'installer successivement dans l'écosystème initialement vide. Les espèces s'assemblent progressivement. Le réseau trophique et le fonctionnement de l'écosystème se modifient au cours du processus d'assemblage en interagissant mutuellement. J'intègre dans ce modèle les apports de la théorie métabolique en représentant les taux biologiques des espèces à l'aide de relations allométriques avec leur masse corporelle. Les interactions de consommation dépendent aussi de la masse corporelle (on suppose que les espèces mangent en général des espèces plus petites qu'elles). Cela permet de relier explicitement le fonctionnement des écosystèmes au métabolisme et aux traits des espèces. La synthèse écologie des communautés – écologie des écosystèmes dans le modèle se traduit par l'intégration explicite des nutriments inorganiques. De plus, je considère les populations des espèces non en terme de nombre d'individus (comme dans les modèles démographiques) mais en terme de stock de nutriments organiques, ou biomasse de l'espèce (chaque espèce est représentée par un compartiment dans l'écosystème).

Un point sémantique s'impose quant au processus d'assemblage : quand je parle d'assemblage ou de construction des réseaux trophiques, je désigne plus particulièrement la mise en place de l'architecture du réseau d'interactions. Je me centre alors sur l'étude de ses propriétés, comprenant entre autres la richesse spécifique, les proportions des différents niveaux trophiques, et la distribution des traits des espèces. Quand je parle d'assemblage ou de développement des écosystèmes, j'inclue l'interaction avec le fonctionnement et l'étude des propriétés globale de l'écosystème tels que la biomasse, la production ou la

productivité. La séparation entre propriétés du réseau trophique et de l'écosystème est un héritage des approches distinctes « communauté » et « écosystème » de l'écologie. C'est pratique pour examiner les mécanismes de rétroactions émergeant des processus qui interagissent entre différentes échelles d'organisation, et pour se référer à la littérature. Cependant, les propriétés de l'écosystème incluent celles du réseau trophique, et le développement de l'écosystème inclue l'assemblage du réseau trophique.

Je regroupe ces trois chapitres sous le chapeau commun d'« assemblage des écosystèmes » (bien que le chapitre 3 n'évoque le fonctionnement que dans la discussion), parce qu'ils constituent des étapes progressives dans l'étude des mécanismes d'assemblage des espèces et de ses interactions avec le fonctionnement des écosystèmes.

Chapitre 3 – Assemblage des écosystèmes (1) Mécanisme de sélection écologique

Au cours du processus d'assemblage, les nouvelles espèces qui arrivent (colonisateurs) entrent en compétition avec les espèces résidentes de l'écosystème. Ces interactions peuvent conduire à ce que les colonisateurs parviennent ou non à s'installer, coexistent avec les résidents, ou provoquent des extinctions. L'issue dépend des traits des espèces qui définissent leur capacité à utiliser la ressource et à supporter la pression de prédation (*e.g.* la masse corporelle, qui témoigne de leur productivité, et leur efficacité à convertir leur ressource en nouvelle biomasse). Les issues successives de ces évènements de compétition modifient progressivement la distribution des traits des espèces dans le réseau trophique au cours de l'assemblage, ce qui se répercute sur le fonctionnement des écosystèmes. Analyser ce processus, que je définis sous le nom de « sélection écologique », est donc une étape essentielle pour comprendre l'interaction entre réseau trophique et fonctionnement de l'écosystème au cours de l'assemblage des écosystèmes.

Je propose donc d'étudier, avec les outils classiques de la théorie consommateur-ressource (théorie du ratio de ressources et de la compétition apparente : Tilman 1982,

Chase et Leibold 2003), comment ce processus de sélection écologique affecte les traits des espèces dans les modèles intégrant les contraintes bioénergétiques.

Chapitre 4 – Assemblage des écosystèmes (2) Effet du timing d'assemblage

La discipline de l'assemblage des communautés a principalement cherché à expliquer comment, et dans quel cas, l'ordre de l'arrivée des espèces (séquence d'assemblage) pouvait générer des communautés ayant des diversités et des structures différentes à partir du même groupe de colonisateurs potentiels. Les modèles étudiant ces effets de contingences historiques considèrent généralement que les espèces arrivent une à une, et que l'écosystème atteint un état stationnaire entre chaque colonisation.

Dans ce chapitre, je teste si le timing de l'assemblage (incluant la vitesse à laquelle les espèces arrivent, et le nombre de colonisateurs simultanés) peut faire diverger l'assemblage vers des réseaux trophiques différents, indépendamment de la séquence d'assemblage. En plus de la richesse en espèces, j'analyse comment ces caractéristiques du processus d'assemblage influencent la distribution des traits des espèces et les propriétés de l'écosystème.

Chapitre 5 – Assemblage des écosystèmes (3) Recyclage et boucle d'interaction entre biodiversité et fonctionnement des écosystèmes

La relation entre la diversité et le fonctionnement des écosystèmes (BEF) a été abordée par des perspectives différentes, avec l'écologie des écosystèmes et l'écologie des communautés. La première a étudié comment la fertilité des écosystèmes influence leur diversité (Waide *et al.* 1999). La seconde a étudié comment la diversité influence la productivité des écosystèmes pour des fertilités similaires (Hector *et al.* 1999, Tilman *et al.* 2001). Une synthèse conceptuelle de ces résultats a été réalisée (Loreau *et al.* 2001) et quelques modèles de réseaux trophiques simples ont permis de poser des bases

mécanistiques à la compréhension de la relation BEF (Loreau 1998b, 2001, Thébault et Loreau 2003, 2005, 2006).

Dans ce chapitre, je propose d'étudier la relation BEF dans le cadre de l'assemblage des écosystèmes complexes. J'intègre la boucle du recyclage par un couplage entre un réseau trophique autotrophe (basé sur les producteurs primaires) et un réseau trophique détritivore. Le fonctionnement de l'écosystème rétroagit sur la diversité en espèces au cours du processus d'assemblage via le recyclage de la biomasse. Comme pour les chapitres 3 et 4, l'intégration des contraintes bioénergétiques permet d'expliquer le fonctionnement des écosystèmes par les traits des espèces. Cette nouvelle approche combine les perspectives de l'assemblage des réseaux trophiques et du développement des écosystèmes pour comprendre de façon mécaniste l'interaction dynamique entre biodiversité et fonctionnement des écosystèmes.

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CHAPITRE 1
INTERACTIONS ENTRE RESSOURCES INORGANIQUES ET STRATEGIES DE CROISSANCE DES ESPECES

1.1 TITRE DE L'ARTICLE

Évolution de bactéries super-compétitrices pour le phosphore par une sélection à faibles densités de population

1.2 RÉSUMÉ

Une croissance rapide peut être une stratégie adéquate en conditions d'abondance de ressources. Cependant la forte demande en phosphore (P) et en azote (N) des fonctions de biosynthèse pourrait diminuer la compétitivité des espèces à croissance rapide pour ces nutriments, comme le suggère l'hypothèse du taux de croissance (Growth Rate Hypothesis, GRH). A l'inverse, des petites tailles d'organismes pourraient induire une relation positive entre les capacités de croissance et d'acquisition des nutriments. L'évolution expérimentale permet de tester si la physiologie des cellules est réellement à l'origine de ces compromis entre capacité de croissance et d'acquisition des nutriments en contrôlant au maximum les autres facteurs. Dans cette étude, nous testons la relation entre taux de croissance maximum *per capita* (μ_{max}) et compétitivité pour P ou N, en faisant évoluer différentes stratégies de croissance à partir d'un ancêtre unique de bactérie *Pseudomonas fluorescens SBW25 mutS*. Nous avons sélectionné les bactéries sur un continuum entre la phase de croissance (faibles densités de populations) et la phase stationnaire (fortes densités de populations), en faisant varier le volume de transfert lors de cultures « en batch » (*i.e.* discontinues), de façon à faire évoluer un gradient de taux de croissance, μ_{max}.

Nous trouvons une forte corrélation positive entre μ_{max} et la compétitivité pour P. Des *super-compétiteurs* pour le phosphore ont été sélectionnés à faibles densités de population,

alors que les bactéries sélectionnées à fortes densités sont simultanément plus lentes à croître et moins compétitives sur le phosphore. En fait, les super-compétiteurs ont des tailles de cellules plus petites, ce qui suggère que leur fort ratio surface : volume leur donne un avantage compétitif pour l'acquisition des nutriments. Au contraire, la sélection à fortes densités de population a induit des fluctuations importantes dans l'approvisionnement des ressources, ce qui a favorisé la coexistence de stratégies diversifiées, exprimées au travers d'une distribution de taille de cellules plus étendue. Ces résultats appuient d'autres récents résultats théoriques et expérimentaux trouvés sur le phytoplancton. Nous montrons qu'au-delà de la plasticité, les populations unicellulaires peuvent répondre rapidement à des variations densité-dépendantes du régime d'approvisionnement des nutriments, à travers l'évolution conjointe de leur taille, de leur taux de croissance intrinsèque et de leur niche stœchiométrique.

Cet article intitulé « Selection at low densities evolves super-competitor bacteria for phosphorus » a été co-rédigé par le chercheur Tanguy Daufresne, mes directeurs de thèse Nicolas Mouquet et Dominique Gravel, et moi-même. Le manuscrit est actuellement proche d'être soumis pour publication dans la revue *Functional Ecology*. Un affinage du style, et du titre sont prévus.

En tant que première auteure, j'ai réalisé la recherche bibliographique, la plus grande part des expériences (notamment la totalité de l'expérience d'évolution), les analyses statistiques et l'essentiel de la rédaction. J'ai également obtenu un financement de la part du Conseil Scientifique de l'Université Montpellier 2 lors de l'appel à projet scientifique 2011 (projet BAMBIS : BActerian Metaecosystem and BIodiversity of Stoichiometric niches). Tanguy Daufresne, second auteur, et Nicolas Mouquet, dernier auteur, ont fourni l'idée originale, constituant une des parties expérimentales de leur projet d'ANR NOE. Le présent travail a ainsi pu bénéficié d'expériences pilotes et de ressources de laboratoires du projet NOE. Corinne Bouvier, Thierry Bouvier, Marine Combe, Claire Barbera et Franck Poly, respectivement 4ème, 5ème, 6ème, 7ème et 8ème auteurs, ont participé aux mises au point expérimentales et aux expériences sur les souches évoluées (ainsi que Marie Vasse et Clara

Torres-Barceló, citées dans les remerciements). Tanguy Daufresne, second auteur, et Nicolas Mouquet, dernier auteur, ont aussi contribué à l'élaboration du design expérimental, à la réflexion autour des résultats et à la rédaction, conjointement avec Dominique Gravel, 3ème auteur, et moi-même.

1.3 TITLE

Selection at low densities evolves super-competitor bacteria for phosphorus

1.4 ABSTRACT

Growing fast may be a successful strategy in conditions of high resource abundance. However the high phosphorus (P) and nitrogen (N) requirements of biosynthesis functions may alter species competitive abilities for these nutrients as suggested by the Growth Rate Hypothesis (GRH). Conversely, smaller sizes of organisms may induce positive relationships between growth and acquisition abilities. Experimental evolution allows testing if cell physiology is responsible for these relationships, all other factors being controlled. We tested the relationship between maximum per capita growth rate (μ_{max}) and competitive ability for P and N by evolving different growth strategies from a single ancestor of bacterium *Pseudomonas fluorescens*. We selected bacteria on a continuum between the growing phase (low density) and the stationary phase (high density), by varying the volumes transferred in batch cultures, to evolve a gradient of μ_{max}. We found a strong positive correlation between μ_{max} and competitive ability for P. Super-competitors for P were selected at low density, whereas strains selected at high density were both slower growers and worse competitors for P. Actually, super-competitors had smaller cell sizes, suggesting that a higher surface: volume ratio gave them a competitive advantage in nutrient acquisition. Conversely, selection at high density induced fluctuations in nutrient supply, which favored the coexistence of diverse growth strategies, with an extended cell size distribution. These results give support to recent findings on phytoplankton. We showed that, beyond plasticity, unicellular populations can respond rapidly to density-dependent variations in nutrient supply regimes, through a joint evolution of their size, their intrinsic growth rate and their stoichiometric niche.

1.5 INTRODUCTION

Species persistence in variable environments depends on the adaptation of their growth strategy to the local conditions of resources and on their competitive abilities for these resources. Nutrient requirements are responsible for the evolution of growth strategies *via* the physiological constrains linking intrinsic growth rate and competitive ability for essential nutrients (Arendt 1997, Kay *et al.* 2005). Here we investigated experimentally the emergence of growth strategies by evolution.

Growing rapidly can be the major axis of an optimal life-history strategy when resources are abundant or fluctuating (Litchman and Klausmeier 2001). Species growing fast can monopolize the resources and outcompete their competitors. For instance, ruderal plants (*sensu* Grime 1977) are efficient colonizers of frequently disturbed environments thanks to their ability to grow fast where disturbances prevent competitive species to deplete nutrients (Lavorel et al. 1999). Similarly, in areas receiving heavy loads of inorganic nutrients, cyanobacteria or microalgae growing fast may create blooms by escaping predator regulation (Riemann *et al.* 2000, Smith 2003). However the capacity to grow fast implies that a greater part of the resources are allocated to biosynthesis, potentially at the expense of others essential biological functions such as defense or resource acquisition (see Arendt 1997 for a review, Klausmeier *et al.* 2004). Therefore, the maximization of growth rate might be detrimental to organisms' persistence on other fitness axes such as resistance to predation (Lankford *et al.* 2001, Stamps 2007), or to resource limitation (Boyce 1984, Sommer 1986). In the absence of disturbances, consumer-resource theory predicts that the species whose traits allow maintaining a viable population with the lowest equilibrium density of the resource (R*) will exclude all its competitors independently of their respective growth rates (R* rule: Tilman 1977, 1980, Tilman *et al.* 1981, Holm and Armstrong 1981, Kilham 1986). As a consequence, in a constant environment and with a limited resource, favoring nutrient acquisition should be a more successful long-term strategy than maximizing intrinsic growth rate. A trade-off therefore exists between a strategy maximizing the resource acquisition abilities in a stable environment and a strategy maximizing the growth rate in a variable environment

(respectively "*gleaner*" and "*opportunist*" strategies sensu Grover 1990, Litchman and Klausmeier 2001, 2008).

Ecological stoichiometry stressed the importance of biochemical constrains in producing trade-offs between life-history traits (Sterner and Elser 2002). The biological functions prioritized by a given strategy (such as biosynthesis, nutrient acquisition, *etc.*) need to be fueled with appropriate resources. This would lead to specific nutrient requirements imposed by the molecules associated to the function. Notably, the Growth Rate Hypothesis ("GRH", Elser *et al.* 2000) states that growing faster requires greater amounts of RNA to sustain biosynthesis activity (Sutcliffe 1970). This results in greater relative content of phosphorus in organisms growing fast owing to the richness of nucleic acids in phosphorus, and to a lesser extent of nitrogen (Sterner and Elser 2002, Makino *et al.* 2003, Kyle *et al.* 2006). Some experiments have shown that phosphorus limitation reduces both relative growth rate and intracellular RNA (Acharya *et al.* 2004). The logical corollary is that species growing fast should be less tolerant to phosphorus deficit than slow growing species (Klausmeier *et al.* 2004), and also should be less competitive in cases where phosphorus is the limiting nutrient (Sommer 1986). Consequently, we should observe a negative correlation between intrinsic growth rate and the competitive ability for phosphorus. Since nucleic acids are also fairly rich in nitrogen, a similar but weaker trend should also hold for nitrogen.

The observation of stoichiometric trade-offs may however be prevented by the interaction with cell size in unicellular osmotrophs. Smaller organisms are growing faster (Raven 1998) and also have smaller genomes (Gregory 2001, 2005, Hessen *et al.* 2010a, 2013, but see Viera-Silva *et al.* 2010 and Hessen *et al.* 2010b). Both features, are likely to increase the capacity of organism to grow fast by shortening the replication process, and the time needed for cell division (Hessen *et al.* 2010a, 2013). In addition, smaller osmotrophs are more efficient to uptake nutrient through diffusion owing to their high surface: volume ratio (Tambi *et al.* 2009). Subsequently, as size is negatively related to nutrient acquisition and negatively related to intrinsic growth rate, this might allow the emergence of hereafter

called super-competitor species, both growing fast and good competitors for N or P (Litchman 2007, Edwards *et al.* 2011).

High growth rates should be selected in an environment where resources are not limiting, for instance at low population density in a freshly disturbed environment (Litchman and Klausmeier 2001, Grether *et al.* 2001). The GRH predicts a low competitive ability for phosphorus should be promoted in such conditions (Sommer 1986, Elser *et al.* 2000). Alternatively, we expect selection of resource acquisition abilities when resources become limiting (Reynolds 2006), for instance as population density increase in a constant environment. Therefore, the strength of density-dependent selection (*i.e.* selection at higher versus lower population densities) may determine the evolution of growth strategies along a continuum from the maximization of intrinsic growth rate to those of competitive ability for P (and N). However, since cell size is related to both, growth and acquisition abilities (Litchman *et al.* 2009), the observation of such trade-offs may depend on the relative strength of the selection for cell size (Edwards *et al.* 2011, 2013).

Our objective here is to investigate experimentally the relationship between the capacity to grow fast and the competitive ability for essential resources, N and P. We take advantage of the rapid growth of bacteria to study the evolution of growth strategies, which allows us to control for other potential confounding factors. We investigate the emergence of specific growth strategies in bacterium *Pseudomonas fluorescens* SBW25 from a single clone experiencing different intensities of density-dependent selection. Low density-dependent selection should evolve strains with higher growth rates conversely to high density-dependent selection. From this diversification of growth rates we test the two hypotheses presented above, for bacteria selected at different densities:

(1) According to the GRH, fast growing bacteria should display a low competitive ability for phosphorus (and to a lower extent for nitrogen), compared to slow growing ones;
(2) According to the size hypothesis exposed by Edward and colleagues (2011), fast growing bacteria should be of smaller cell sizes, and should display greater competitive abilities for phosphorus and nitrogen, than slow growing bacteria.

1.6 METHODS

We experimentally evolved strains of a single bacterial clone of *Pseudomonas fluorescens* SBW25 at different intensities of density-dependent selection. We then estimated the maximum per capita growth rate of the evolved strains, μ_{max}, and their competitive ability for N and P from 48-hours-kinetics on low-P and low-N medium. We also scanned populations of our ancestor and evolved strains by flow-cytometry to compare their relative cell sizes. We finally analyzed the correlations between μ_{max}, competitive ability and relative size.

1.6.1 Evolution experiment

We started from a single clone of *Pseudomonas fluorescens SBW25–* to limit the initial variability of μ_{max}. We used a hyper-mutator strain *mutS-* (a constructed SBW25 mutS knockout mutant), with a mutation rate of c. 10^{-5} per base pair, per generation instead of c. 5×10^{-7} for the WT (Pal et al. 2007, Escobar-Paramo *et al.* 2012). We first cultivated the ancestral strain in King's Broth medium during 12 hours. We plated the population and selected at random 6 colonies to be our 6 ancestors for the evolution experiment. During the evolution experiment, we grew bacteria in NOEmI medium, a medium specially designed to vary independently N and P in later assays (see Appendix A). We evolved our 6 ancestors in batch cultures: during two months we transferred cultures every 48h into new medium to maintain bacterial growth (30 transfers). The evolution treatments consisted of varying the volume of culture transferred from 10^{1} to $10^{-4}\mu$l (figure 1, panel A). After few transfers, populations for which we transferred large volumes spent more time at high population density before being transferred (figure 1, panel B). Indeed, larger volumes of culture transferred makes bacterial dynamics start with higher initial densities. Then the stationary state is reached sooner. In contrast, populations for which we transferred small volumes, were still increasing population density at the time of the transfer (figure 1, panel B). Hence, we selected bacteria on a continuum between the growing phase (low density)

and the stationary phase, or "plateau" (high density). The density-dependent selection increased with the transfer volume.

At the end of the evolution experiment, we realized that half of the evolved strains,

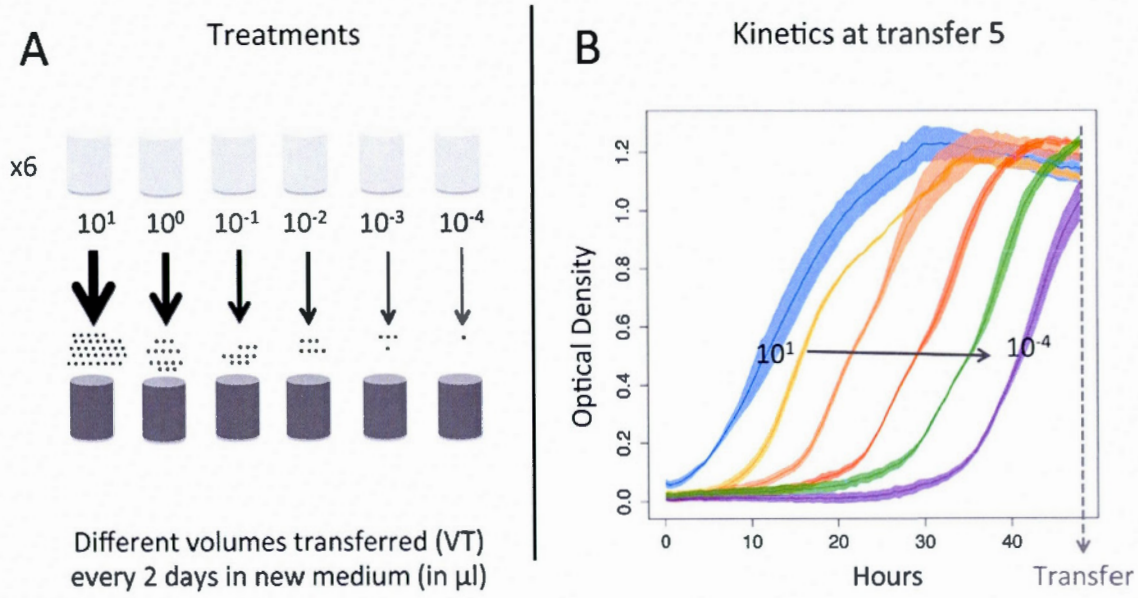

Fig. 1 Evolution Experiment

A, Experimental design: we transferred bacterial cultures every 2 days in new medium. Treatments consisted in varying the volume of transfer from 10 µl to 10^{-4}µl, which corresponds to decreasing numbers of bacteria transferred. This led to a delayed growth between treatments after few transfers: panel B represents time series of strains growth after the fifth transfer. Hours are reported on X-axis and Optical Densities on Y-axis (after removing the blanks, i.e. medium without culture). Optical densities are used as a proxy of microbial biomass. Colors corresponds to evolution treatments: increasing volumes of transfer are represented respectively from the left to the right in blue, yellow, brown, red, green and purple colors. Lines are average values over the 6 evolution replicates of each treatment, and colored areas represent the standard deviation.

those evolved with the highest transfer volume, had fixed wrinkly colony morphotypes (appendix B). This morphotype dominated the air-liquid interface of the medium and likely appeared in response of low oxygen availability at high densities. Since wrinkly

morphotypes are known to make biofilm (Rainey *et al.* 2000), they probably have very different physiological requirements from those of the ancestor (smooth morphotype). Subsequently, to keep comparable strains, we removed from further analyses the following evolution treatments: 10^{1}, 10^{0}, $10^{-1}\mu l$ of volume transferred. Remaining treatments are hereafter called $VT10^{-2}$, $VT10^{-3}$, and $VT10^{-4}$.

1.6.2 Traits measurement

We characterized growth rate and competitive ability for nitrogen and phosphorus. For a given resource, the competitive ability can be characterized by the R^* (Tilman 1982), which represents both minimum resource requirements of the species and the density of the resource when the species as reached equilibrium. For a total quantity of resource T_R, the R^* can be defined as $R^* = T_R - q_R B^*$, where B^* is the biomass of the species at equilibrium and q_R the quota of the resource into the biomass. If the total resource is held constant, then an estimator of the R^* is given by $R^* \propto -q_R B^*$. Data on the stoichiometry of cellular composition for each strain shows that the quotas of nitrogen and phosphorus, respectively q_N and q_P, were independent from the maximum per capita growth rate μ_{max} (Appendix C). We therefore assumed that all of our evolved strains have the same q_N and q_P. Subsequently, for each of the two resources N and P we used the biomass at equilibrium when the resource is limiting as a proxy to estimate the N^* and the P^*.

We performed 70 hour cultures for which either nitrogen or phosphorus was the limiting resource (low-N and low-P media). We extracted from the growth curves a measure of the μ_{max} and a proxy of the biomass at equilibrium (details on the statistics in the next section). We used two diluted versions of the evolution medium, one where phosphorus was diluted by 60 (low-P medium), and one where nitrogen was diluted by 3 (low-N medium), all else being equal. We ran five replicates for each of the 24 strains (6 ancestors + 3 treatments x 6 evolution replicates) on each media. Biomass was measured by the maximum optical density (OD_{max}) reached during a 70 hours growth period (time chosen such that the plateau can be reached even despite the low growth rates on low-P

medium). Thereby the competitive ability for one resource R is approximated by $-OD_{max}^{(low-R)}$. The maximum per capita growth rate, μ_{max}, has been calculated as the maximum gain of *OD* units by hour and by *OD* unit. The μ_{max} of each strain was different for the two media, since the limitation of phosphorus slows down the growth rate, whatever the intrinsic growth rate of the strain. However, the realized μ_{max} on low-P and low-N media were positively correlated (Spearman's rank correlation: $\rho = 0.65, n = 18, P < 0.01$; Table 2, appendix D).

We compared the relative average cell size by flow cytometry proxys (FSC-H). We grew 6 replicate populations in King's Broth medium for each of the 18 evolved strain and 6 ancestors, during 24 hours. The growth time has been chosen so that the populations have passed the exponential phase for the cell size to be more representative of strains characteristics (with cells of all physiological stages and not only small cells in a division stage). Some replicates of one strain of the VT 10^{-3}µl treatment did not grow enough and have been removed them from the analysis. We recorded the FSC-H parameter for 50000 cytometer events in diluted samples of each population (such to obtain 800 to 1500 events / second). As a proxy for strain cell size, we averaged the FSC-H geometric mean of the 6 replicates. Geometric mean better captures the diversity of population with large size distribution than do arithmetic mean, because it is less sensitive to high values. However we found similar results with arithmetic means. We also analyzed the effect of evolution treatments on the variance of cell size distributions, with a proxy obtained by multiplying the geometric mean by the coefficient of variation.

1.6.3 Statistical analyses

We performed Kruskal–Wallis rank sum tests for each trait against evolution treatments (Table 1) to assess the effect of our selection treatments on traits (μ_{max}, OD_{max} and size). We used non – parametric tests, because some data were either not normally distributed (Shapiro's test) or their variances were heterogeneous (Bartlett's test). We were not able to use nested models with non-parametric tests. We therefore applied the tests on

replicates means to avoid pseudo-replication. We then used post-hoc multiple comparison tests, with the function kruskalmc of the pgirmess R package 1.5.9 (Giraudoux 2014), to determine which traits were different from one another in average according to treatments (based on the methods in Siegel and Castellan 1988). We performed Spearman's

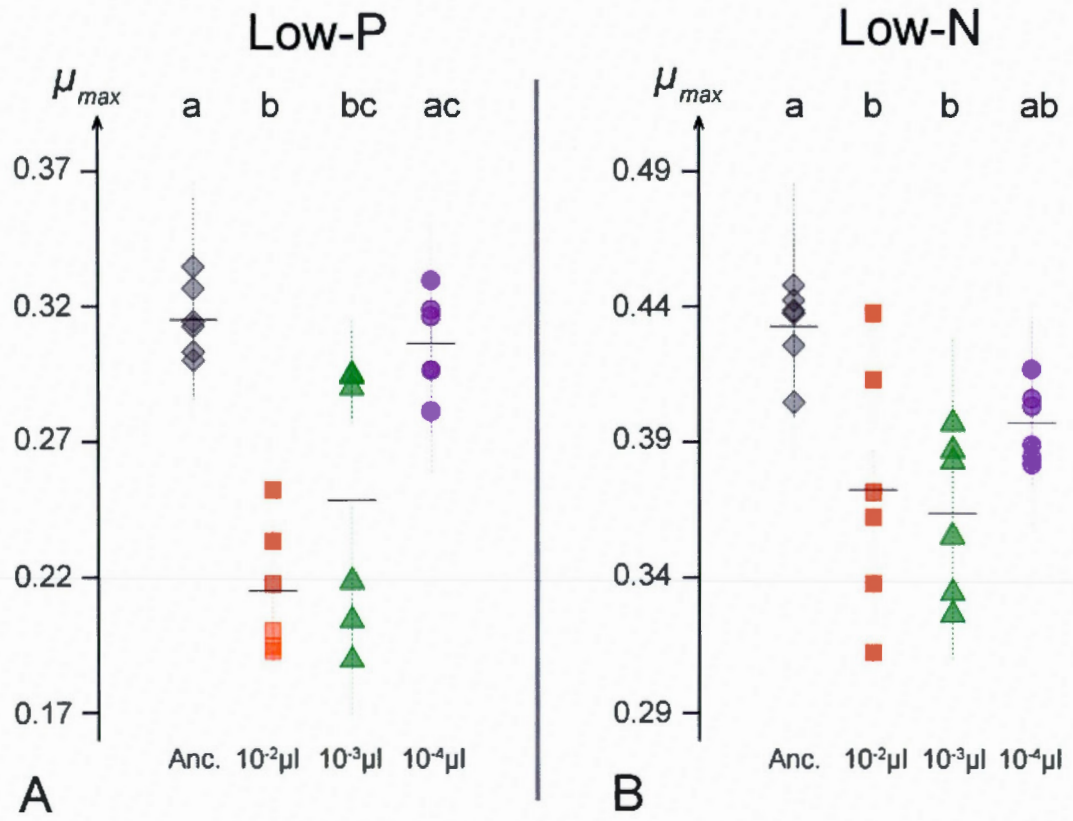

Fig. 2 Maximum per capita growth rates of ancestors (grey diamonds) and evolved strains on low-P (panel A) and low-N (panel B) media

Labels indicate volumes of transfer (VT) used for the different evolution treatments of corresponding strains: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$, are and purple circles for $VT10^{-4}$. Shapes represent means of 5 replicate measures for each of the 6 evolution replicates by treatment. Bars represent the mean for the treatment. Variances were not homogenous (Bartlett test; on Low-P: $\chi^2 = 9.32, n = 24, df = 3, P < 0.05$; on Low-N: $\chi^2 = 8.56, n = 24, df = 3, P < 0.05$). Letters refers to significantly different means according to non-parametric tests of multiple mean comparaisons after significant Kruskall-Wallis' test on means (Siegel and Castellan 1988).

correlation tests on ranks to characterize the relationships between traits (data on low-P medium were not normally distributed). We also performed an ANOVA to test the effects of treatments on the spread of cell size distributions (residuals were normally distributed and variance homogenous, Table 2). We then used post-doc Tukey's HSD test to analyze the differences according to treatments.

1.7 RESULTS

The evolution experiment successfully diversified the μ_{max} on low-P and low-N medium compared to the ancestors (figure 2). The maximum per capita growth rates μ_{max} were significantly different between the ancestors and the strains selected at high densities, $VT10^{-2}$ and $VT10^{-3}$, but not between ancestors and bacteria selected at low density ($VT10^{-4}$) (Table 1 and figure 2). Among evolved strains, populations having been transferred during the growing phase ($VT10^{-4}$ treatment) displayed greater μ_{max} on low-P medium than populations selected at the stationary phase ($VT10^{-2}$) (Kruskal-Wallis' test: $P < 0.01$). There were however no significant differences of μ_{max} between treatments on low-N medium dependence (Kruskal-Wallis' test: $P = 0.182$). In addition, phosphorus limitation slowed down the μ_{max} of all strains, compared to their growth when phosphorus was not limiting (means are significantly different: Mann & Whitney's test, P<0.0001, and $\mu_{max}^{(low-P)}(0.27) < \mu_{max}^{(low-N)}(0.39)$).

The variances of μ_{max} differed regardless of the medium (Bartlett's tests: on Low-P: $\chi^2 = 9.32, n = 24, df = 3, P < 0.05$; on Low-N: $\chi^2 = 8.56, n = 24, df = 3, P < 0.05$). The variance of μ_{max} was larger for the bacteria grown at high volume transfer compared to those grown at low volume transfer ($VT10^{-4}$). On low-P medium, μ_{max} were more variable for $VT10^{-3}$ than for $VT10^{-4}$ treatments ($F = 7.57, df = 5, P < 0.05$); on low-N medium, μ_{max} were more variable for $VT10^{-2}$ than for $VT10^{-4}$ treatments ($F = 11.20, df = 5, P < 0.05$).

Table 1 Kruskal-Wallis rank tests on the effects of evolution treatments on traits
Letters in the last column refer to significantly different means between treatments according to post-hoc non-parametric tests of multiple mean comparisons (method in Siegel and Castellan 1988). Treatments are: Ancestors, $VT10^{-2}$, $VT10^{-3}$, $VT10^{-4}$.

Data	n	df	χ^2	P		Multiple comparisons
On Low-P Medium						
μ_{max}~ treatments (with ancestors)	24	3	16.63	<0.001	**	a b bc ac
μ_{max}~ treatments	18	2	15.46	<0.010	*	a ab b
OD_{max}~ treatments (with ancestors)	24	3	17.64	<0.001	**	ab a ab b
OD_{max}~ treatments	18	2	13.13	<0.010	*	a ab b
On Low-N Medium						
μ_{max}~ treatments (with ancestors)	24	3	12.78	<0.010	*	a b b ab
μ_{max}~ treatments	18	2	3.40	0.182	-	
OD_{max}~ treatments (with ancestors)	24	3	1.77	0.621	-	
OD_{max}~ treatments	18	2	1.20	0.548	-	
Cell Size ~ treatments (with ancestors)	24	3	17.70	<0.001	**	ab a ab b
Cell Size ~ treatments	18	2	14.36	<0.001	**	a ab b

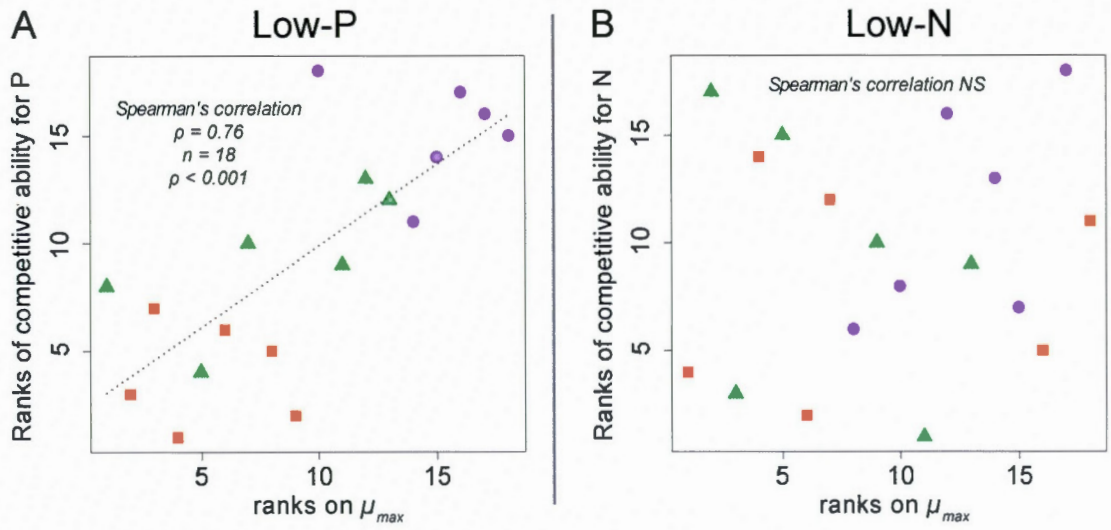

Fig. 3 Relationship between ranks of competitive abilities for P (panel A) and N (panel B) and of maximum per capita growth rate

Competitive ability is approximated with the maximum optical density (OD_{max}) obtained during 70 hours of bacterial growth on either Low-N or low-P medium. Ranks are computed on the mean of 5 replicated kinetics for each evolved strain, performed on 4 days. Shapes and colors of the points code for the different evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$.

We found a positive relationship between $\mu_{max}^{(low-P)}$ and $OD_{max}^{(low-P)}$ when bacteria were P-limited (fig.3, panel A; Spearman's correlation test on ranks: $\rho = 0.76, n = 18, P < 0.001$). Bacteria grown with low volumes of transfer ($VT10^{-4}$) displayed greater maximum growth rates and greater competitive ability for phosphorus than the strains grown under high volume transfer (Table 1; Kruskal-Wallis' test for μ_{max}: $P < 0.01$; multiple comparison test gives μ_{max} different between $VT10^{-2}$ and $VT10^{-4}$ treatments, with $P < 0.01$; Kruskal-Wallis' test for OD_{max}: $P < 0.01$; multiple comparison test gives OD_{max} different between $VT10^{-2}$ and $VT10^{-4}$ treatments, with $P < 0.001$). By contrast, when bacteria were N-limited, no relationship appears between maximal growth rate ($\mu_{max}^{(low-N)}$) and competitive ability for the resource ($OD_{max}^{(low-N)}$) (fig.3, panel B). Finally, we found no significant relationship between the competitive ability for nitrogen ($OD_{max}^{(low-N)}$) and the

competitive ability for phosphorus ($OD_{max}^{(low-P)}$) (Spearman's correlation test on ranks: *P=0.20,* Appendix E).

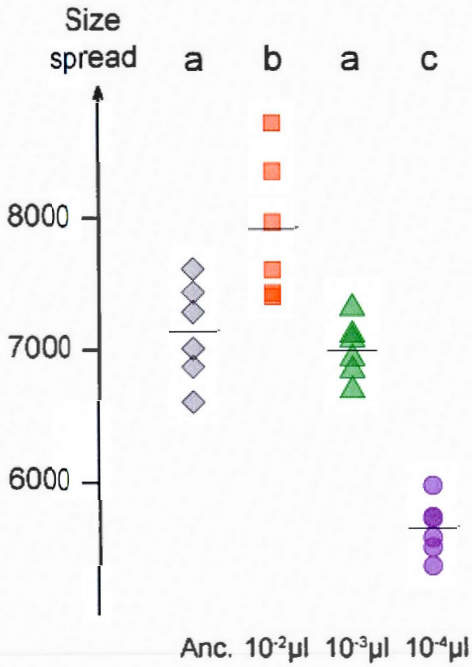

Fig. 4 Spread of cell size distributions of ancestors (grey diamonds) and evolved strains

Labels indicate the volume of transfer (VT) used for the different evolution treatments of corresponding strains: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$, are and purple circles for $VT10^{-4}$. The variability of cell size distributions was approximated by the products of geometric mean and CV of the FSC-H parameter measured by flow-cytometry over 50000 events by population. Shapes represent means of 5 replicate measures for each of the 6 evolution replicate by treatment. Bars represents the mean for the treatment. Letters refers to significantly different means according to post-hoc Tuckey's HSD test of multiple mean comparisons, after significant differences in ANOVA (Table 2).

Table 2 ANOVA for the spread of cell size distribution of evolved strains and ancestors (CV x geometric mean)

The letters in the last column refer to significantly different means between treatments according to post-hoc Tuckey's HSD test. The treatments are: Ancestors, $VT10^{-2}$, $VT10^{-3}$, $VT10^{-4}$.

Source of variation	df	F	P		Tuckey's HSD test
Treatments	3	41	<0.0001	***	a b a c
Residuals	20				

Evolution treatments significantly impacted the average of cell size (Table 1; Kruskal-Wallis' test: $P < 0.001$) and their distribution variance (Table 2: $F_{3,20} = 41; P < 0.0001$; figure 4 see also Appendix F for cell size histograms). The variance of cell size distributions increased with the transfer volume (Table 2, figure 4). The diversification of

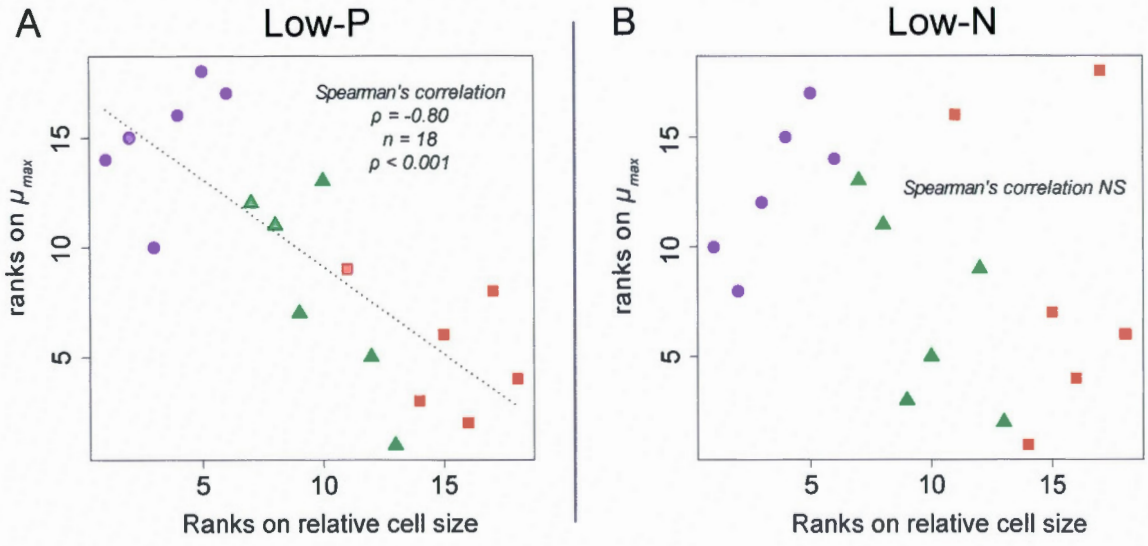

Fig. 5 Relationship between ranks of maximum per capita growth rates μmax on low-P (panel A) and low-N (panel B) media and of average relative size

The relative cell size is approximated with the geometric mean of the FSC-H parameter distribution in the population, measured by flow cytometry over 50 000 events. Ranks are computed on the mean of the replicate measures for each evolved strain (5 replicate populations for the measure of the μ_{max} and 6 replicate populations for the screaning of population cell sizes). Point shapes and colors code for the evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$

cell size was significantly different between $VT10^{-2}$ and ancestors (Tuckey's HSD test: < 0.01). At the opposite, cells transferred with high volumes ($VT10^{-4}$) were less variable than the ancestor (Tuckey's HSD test: < 0.0001). A larger proportion of big cells were found in the high volume treatment in is comparison to the low volume treatment (Table 1). Given the effects of treatments on μ_{max} previously reported on low-P medium, we found a clear negative relationship between the ability to grow fast when phosphorus is limiting and the cell size (Spearman's correlation test on ranks: $\rho = -0.80, n = 18, P < 0.001$, figure 5, panel A). Given the positive relationship between the μ_{max} and the competitive ability for phosphorus (figure 3), the strains with smallest average cell size were also the most competitive for phosphorus (Spearman's correlation test on ranks: $\rho = -0.839, n = 18, P < 0.0001$; Appendix G). Conversely, no relationship was detected between μ_{max} and cell size on N-limited medium (figure 5, panel B), and between cell size and the competitive ability for N (Appendix G).

1.8 DISCUSSION

In summary, super-competitor bacterial populations with small cell sizes were selected at low-density conditions (low VT), displaying higher growth rates and better competitive abilities for phosphorus. Strains with a wider range of cell sizes, including very big cell sizes, were selected at high-density conditions (high VT). Their maximum per capita growth rate was lower than those of bacteria selected at low-density, as well as their competitive ability when P is limiting. However, no significant relationship was found when nitrogen was limiting.

1.8.1 Growth Rate Hypothesis (GRH)

We found that the μ_{max} of all strains decreased with P limitation, which confirms the positive link between P requirements for biosynthesis and maximum growth rate stated by our hypothesis n°1, the GRH (Acharya *et al.* 2004). However this does not implies that the

fast-growing strains were more limited by phosphorus than were slow-growing bacteria. Our selection treatment for fast-growing bacteria evolved strong-competitors for phosphorus (both fast growers and producing more biomass by amount of phosphorus), thereby showing that the potential for fast growth is less straightforwardly linked to competitive ability for the resources involved in biosynthesis than expected from the GRH theory (Sterner and Elser 2002). The density-dependent selection did not simply promote high growth rates and the subsequent resource allocation strategy. It also selected a more integrative phenotypic trait, the relative cell size, which masks and even reverses the trade-off between intrinsic growth and competitive abilities expected from the GRH theory. This result also supports our hypothesis 2, with a "three-way trade-offs" between cell size, growth rate, and competitive ability for phosphorus, similar to those demonstrated by Edwards and colleagues (2011 and 2013) on empirical phytoplankton.

1.8.2 Small size selection and greater intrinsic growth rate

Our evolution treatments impacted the cell size distributions. Fast growing populations display smaller cells sizes. Cell size impacts the growth rate because of shorter time for cell diffusion Hessen *et al.* 2010a, 2013) and greater nutrient acquisition efficiency thanks to their greater surface:volume ratio (Chisholm 1992, Tambi *et al.* 2009, Edwards *et al.* 2011), which is likely to feedback positively on biosynthesis rate. In our experiment, ancestors had a relatively wide cell size distribution despite their isogenic source, due to the growth phases needed for the constitution of ancestor populations (figure 4, appendix F). Interestingly the cell size distribution of our ancestors was wider than the cell size distribution of the selected fast growers. This suggests that the biggest cells grew too slowly to persist when the transfers occurred too early in the growing phase. Their abundance may have been so low at the time of transfer that they finally have been excluded along the experiment. This leaded to a reduction of the cell size diversity. Given this close relationship between small sizes, ability to grow fast and nutrient acquisition evoked above, it is not surprising that small size super-competitor populations emerge from the selection at the growing phase (Litchman *et al.* 2009, Edwards *et al.* 2011).

1.8.3 Why large bacteria are selected at high population densities

If small cells compete better for resource acquisition, then why the proportion of large individuals increased for population transferred when they reached high densities? At high densities, nutrient concentration would drop to very low levels and the greater acquisition capacity of small cells should favor them. However, we observe that, even if small individuals were still abundant, they coexist with an increased proportion of large ones at the high volume transfer treatment. This can be explained by the variability of resource supply between two transfers. When the transfer occurs after reaching maximal density, cells suffer long periods of starvation before the next supply of new rich medium. Pulses of nutrient supply may allow the persistence of large individuals able to store nutrients. Many bacteria have the capacity to stock rich-P polyphosphates in dense granules (Kulaev *et al.* 1999, Kornberg *et al.* 1999, Zhang *et al.* 2002, Rao *et al.* 2009). The P-rich evolution medium (appendix A, Table A3) might have allowed the apparition of such storage capacity (Makino and Cotner 2004), which is a known mechanism favoring coexistence in temporally fluctuating environments (Grover 1991, 2011, Edwards *et al.* 2013). The luxury consumption in periods of resource abundance would fuel growth and maintenance in periods of scarcity. Luxury consumption has also been proposed to be an optimal competitive strategy leading to the starvation of non-storing competitors (De Mazancourt and Schwartz 2010). In addition, Litchman *et al.* (2009) demonstrated that small and big cells could coexist for intermediate frequencies of nutrient pulses. Their model of diatom dynamics successfully reproduces the bimodal size distribution of marine diatoms, which are subject to pulse nutrient loads in upwelling areas. Conversely, diatoms are significantly smaller in freshwater systems. In lakes, nutrient supply regimes are more continuous and smaller cells are found both fastest growers and most competitive for nutrients. Similarly in our system, the bacteria selected during the growing phase experienced more continuous supply (medium less depleted at the time of the transfer). Therefore smallest bacteria are favored, while large bacteria, might persist by using their reserves for maintenance or stress response when nutrients become scarce (Rao and Kornberg 1996, Kulaev and Kulakovskaya 2000, Achbergerová and Nahalka 2011).

1.8.4 Strategy diversification occurs at high densities

In addition to a wider size spectrum, bacterial populations selected at high densities also display more variable growth rates compared to those selected at lower densities. Our selection treatments have induced a variation of nutrient supply amplitudes and starvation periods. Populations selected at high densities experienced stronger disturbance regimes, which allowed the coexistence of small and big cells. In contrast, because resources were less limited during the growing phase, making small bacteria dominant, selection at low densities has created a bottleneck for growth strategies. These variations in strategy diversity with the nutrient supply regimes partly matches with the intermediate disturbance hypothesis ("IDH"; Connell 1978, Molino and Sabatier 2001), which states that diversity peaks at intermediate regimes of disturbance. Small variations in nutrient supply (selection in growing phase) promote the emergence of super-competitors, whereas pulsed nutrient supply (selection at the plateau) promotes the coexistence of both good competitors (small cells) and starvation–resistant bacteria (big cells). Interestingly, for selection treatments at even larger transfer volumes (VT10 to $VT10^{-1}$ treatments, removed from the analysis), strategy diversity does not decrease. On the contrary, we selected different morphotypes (Appendix B). For only one axis of disturbance, IDH would predict diversity to decrease at high disturbance regimes. Only the most adapted to the disturbance are expected to persist. Actually, for long times under very high bacterial densities, not only nutrient are depleted but also oxygen. Therefore our very low nutrient conditions created a novel niche axis and the emergence of oxygen-acquisition specialists (wrinkly morphotypes).

1.8.5 Absence of relationships between μ_{max} on low-N medium, competitive ability for N and cell size

Surprisingly, no relationships were found between traits measured on low-N medium (μ_{max} and proxy for N*), and between these traits and relative cell size. According to Edwards and colleagues' results for phytoplankton (2011), we expected to obtain a *three-*

way trade-off between competitive abilities for N and P and cell size, where, in particular, competitive abilities for N would correlate negatively with size (as for competitive ability for P). Conversely, some strains had relatively large cell sizes and both grow the fastest on Low-N medium and were highly competitive for nitrogen (Appendix G, figure G panel 2). We have no explanation for this observation based on our data but we provide hypotheses. Polyphosphates stored in big cells may be mobilized for cell motility (Rashid and Kornberg 2000) and may increase the capture of scarce nitrogen, which in turn would feedback positively on phosphorus acquisition (Hessen *et al.* 2007, Perini and Bracken 2014). This may increase the μ_{max} and N* of big cells relative to others, only in the case of phosphorus abundance. Another possibility involves an increase in the relative allocation in growth machinery under of nitrogen scarcity, because of a relatively higher nitrogen cost of uptake machinery. This mechanism would thus maximize nutrient use efficiency (NUE), invalidating the GRH prediction of a trade-off between growth rate and competitive ability for nitrogen (Franklin *et al.* 2011). In the low-N medium, P might be non-limiting as growth starts, in phase during which the maximum per capita growth rate is measured. The acquisition abilities of small cells may not be a significant advantage for growth, and μ_{max} may be more or less independent from size cell and similar between treatments. The limitation of phosphorus uptake due to nitrogen scarcity (Hessen *et al.* 2007, Perini and Bracken 2014) may then limit the relative advantage of small fast-growing cells for nutrient acquisition at high densities, and temper the differences between treatments of competitive abilities for N.

1.8.6 Evolving ecological strategies

Common approaches to characterize the physiological constraints linking growth rate and competitive abilities for nutrients include analyses of these traits on large empirical datasets, or experiments where species are grown in different conditions for nutrient availability. But scarce are the examples of studies showing evolution at work for these traits starting from a single clone. Here we selected ecological strategies from a single

ancestral population. Rapid evolution leads to the selection of super-competitors for phosphorus under low density-dependent selection, whereas high density-dependant selection provokes a diversification of ecological strategies. The evolution of autotroph growth strategy in response to nutrient supply regimes highlights in a novel way phytoplankton fluctuating dynamics. Blooms of small-size phytoplankton generally ended by the increase in grazing pressure by zooplankton, which is followed by the selection of grazing-resistant big-size zooplankton (Gosselain *et al.* 1998, Riemann *et al.* 2000). Our results suggest that a parallel process might also select for plankton size. As the bloom start, nutrient are abundant and small cells are favored because more efficient in nutrient acquisition. Later, high densities may provoke starvation favoring large-size starvation-resistant cells. Species using non-limiting nutrient for their biosynthesis, such as diatoms or cyanobacteria, might evolve big size, adding up starvation and grazing resistance (Thingstad *et al.* 2005). We give an experimental support of the evolution of growth strategies, under density-dependent variation of nutrient supply (Litchman *et al.* 2009).

Our study illustrates the potential of metabolic evolution of organisms in response to environmental constraints (Gresham *et al.* 2008, Notebaart *et al.* 2014), and shows that the adaptation of growth strategies to environmental conditions may depend crucially on population variability (particularly of cell size in osmotrophs). We evolved the stoichiometric niche (*i.e.* competitive abilities for the different nutrients) through its physiological linkage to the intrinsic growth rate (Sterner and Elser 2002), stressing the complex functional constraints underlying growth strategies and species coexistence mechanisms.

1.9 ACKNOWLEDGEMENTS

We greatly thank Clara Torres-Barceló, Marie Vasse, Nadine Guillaumot and Myriam Boyer for their assistance. We also thank Clara Torres-Barcelo, Marie Vasse, Guillaume Martin, Benoît Jaillard and Philippe Deleporte for helpful discussions, Oliver Katz and Pierre Gauzère for suggestions on statistics and Patrice Got for hosting in Ecosym laboratories during preliminary experiments. Cytometry has been performed at the Montpellier RIO Imaging plateform of the Institut de Génétique Moléculaire de Montpellier. The project has been funded by the Conseil Scientifique de l'Université Montpellier 2 (AAP2011 – BAMBIS project), and by NOE ANR. I.G. was supported by a MENRT grant from Ministry of Higher Education and Research of France, the Canada Research Chair Program, the Quebec Center for Biodiversity Science and by the Frontenac program (FQRNT and French consulate at Québec). T.D. was funded by the Institut National de la Recherche Agronomique. D.G. was supported by the NSERC and the Canada Research Chair Program. C.G.-B., T.B., C.B, M.C., F.P. and N.M. were funded by the Centre National de la Recherche Scientifique (CNRS).

1.10 APPENDIX A – EXPERIMENTAL DETAILS

1.10.1 Additional details on the evolution experiment

Bacteria were grown in 96-wells microplates, without agitation at 28°C. Each well was filed with 200µl of bacterial culture. Transfers were performed every 48 hours into new microplates filled with 180µl of new medium. Dilutions were done in order to transfer the quantity of bacterial culture corresponding to the transfer volume defined for each evolution treatment, in a volume of 20µl.

1.10.2 NOEmI medium

Table A1 Basal solutions

	Mass	**distilled H_2O**
Na2HPO4.7H2O 0.5M	53.61g	400ml
NH4Cl 1M	21.40g	400ml
Aces	18.22g	400ml
KCl 0.5M	7.46g	200ml
MgSO4,7H2O 1M	49.30g	200 ml
CaCl2,2H2O 1M	7.35g	50ml
Solution A	2.86 g H3BO3, 1.81 g MnCl2.4H2O, 0.08 g CuSO4.5H2O, 0.049 g Co(NO3)2.6H2O, 0.39 g NaMoO4.2H2O, 0.22 g ZnSO4.7H2O	1000ml
Solution B	0.04g	10 ml HCl 0.01 N
Glycérol 50%	100ml	100ml

Basal solutions are sterilized by autoclave, except solution B, which is filtered using 22µm filters.

Table A2: Assemblage of basal solutions for 400ml of NOEmI medium

Basal solution	Volume
Na2HPO4	55.8 ml
NH4Cl	7.48 ml
CaCl2	40 µl
SolA	400 µl
ACES	32ml
KCl	2.4 ml
Autoclave other solutions added in sterile conditions	
Glycérol 50%	4.86 ml
MgSO4	2ml
SolB 10X	40 µl
Sterile distilled water	Up to 400ml

Table A3: media N:P ratios

Medium	N:P ratios
Evolution medium	0.27: 1
Low-N medium	0.09: 1
Low-P medium	16.09: 1

1.11 APPENDIX B – MORPHOTYPES

We carried on a supplementary experiment to test if we had selected wrinkly morphotypes (W) in addition to the ancestor smooth (S) morphotypes with the three evolution treatments having the largest transfer volumes (VT 10^1, VT 10^0 and VT 10^{-1}µl). *Pseudomonas fluorescens* are known to quickly diversify into 3 specialized morphotypes when oxygen becomes rare (Rainey *et al.* 2000). Therefore we needed to test if the morphotypes in our evolved populations were morphotypes fixed by evolution or only transient morphotypes, appearing during the final assays.

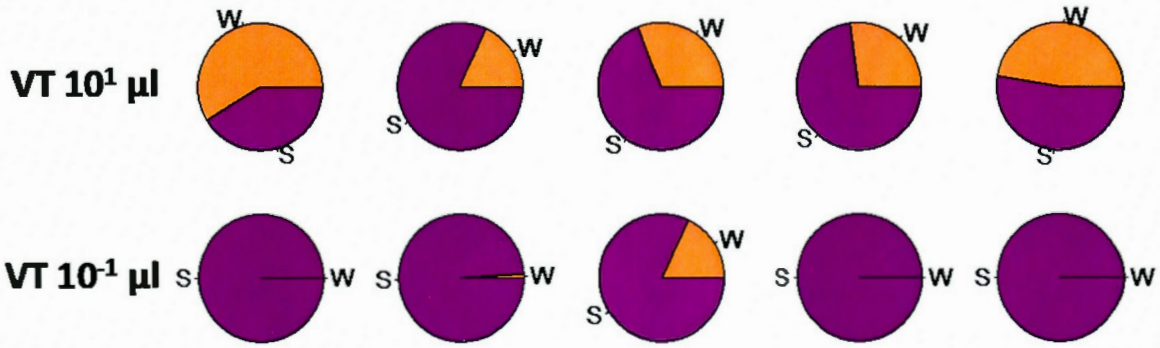

Fig. B1 Proportions of morphotypes at the end of the experiment for evolution treatments volumes of transfer 10^1 and 10^{-1}µl

The pies give the proportion of Smooth (S, purple) and Wrinkly (W, orange) colony morphotypes in the 6 evolved strains of the 2 evolution treatments volumes of transfer (VT) 10^1 and 10^{-1}µl at the end of the evolution experiment. The proportions are obtained from population samples plated in petri dishes filled with appropriate medium (KB agar).

We selected the 2 extreme treatments were Wrinkly were observed at the end of the evolution experiment: VT 10^1 and VT 10^{-1}µl (figure B1). We chose 5 strains (evolution replicates) over the 6 of each evolution treatment. For each of them we picked 10 colonies of Smooth and 10 colonies of Wrinkly to constitute one-morphotype populations (except that for 3 strains of the treatment 10^{-1}µl, no wrinkly colonies were available). We grew them in King's Broth Medium at 28°C in agitated tubes. We plated samples of these

populations at time 0 (t0) and after 48 hours of growth (t48) in petri dishes filled with King's Broth Agar Medium.

Figure B2 shows that the great majority of morphotypes were stable.

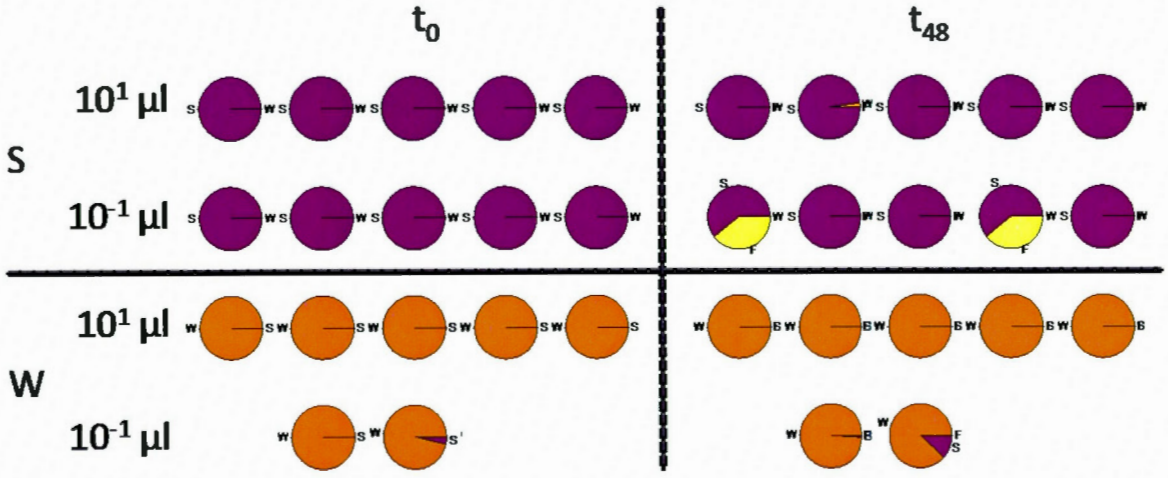

Fig. B2 Proportions of morphotypes at the end of the experiment for evolution treatments volumes of transfer 10^1 and 10^{-1}µl

The pies give the proportion of Smooth (S, purple), Wrinkly (W, orange) and Fuzzy (F, yellow) colony morphotypes in the 6 evolved strains of the 2 evolution treatments volumes of transfer (VT) 10^1 and 10^{-1}µl at the end of the evolution experiment. The proportions are obtained from population samples plated in petri dishes filled with appropriate medium (KB agar).

1.12 APPENDIX C – QUOTAS OF N AND P

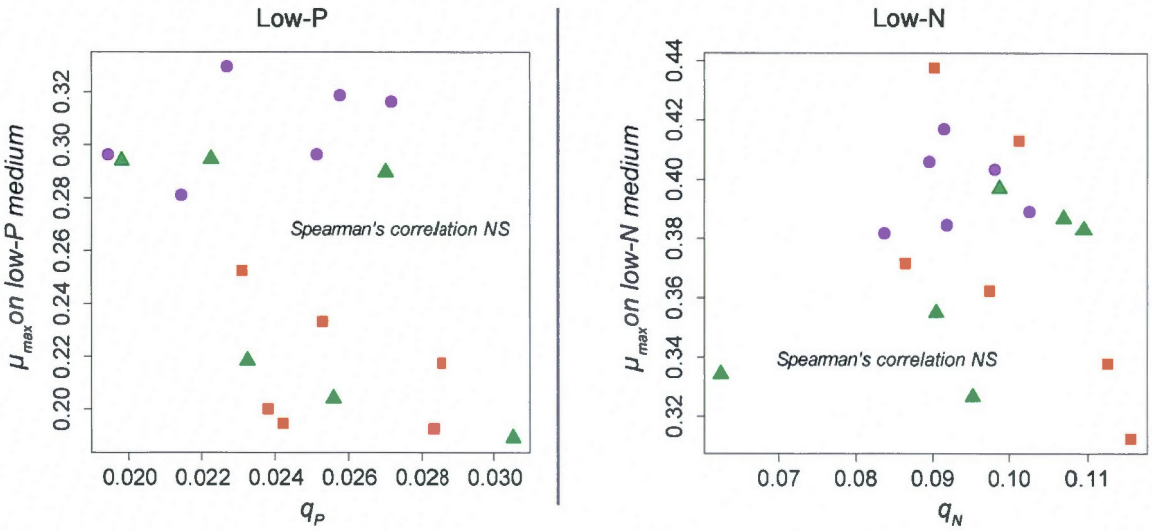

Fig. C Relationship between quota of P (panel 1) or N (panel 2) and μ_{max}

Ranks of μ_{max} are computed on the mean of 5 replicate kinetics for each evolved strain, performed on 4 days. Ranks of *quotas* are computed on the mean of 10 measures for each evolved strain. Shapes and colors of the points code for the different evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$.

1.13 APPENDIX D – MAXIMUM GROWTH RATE

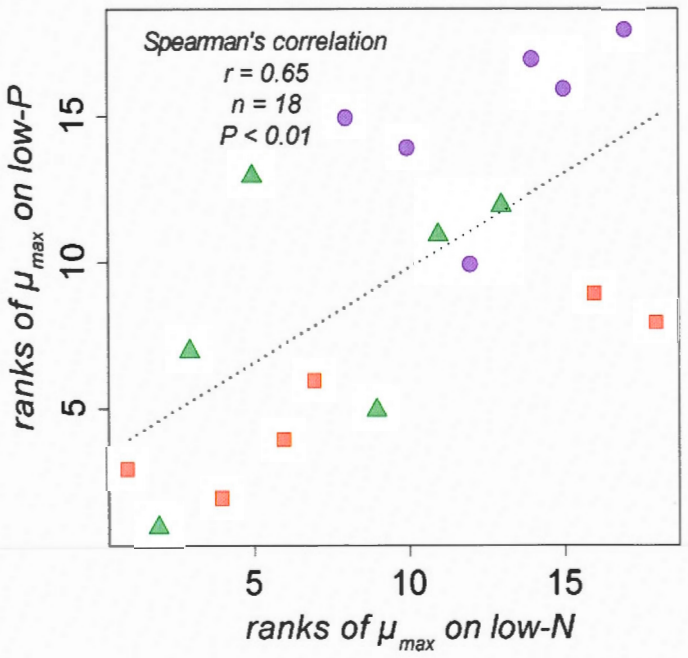

Fig. D Relationship between maximum per capita growth μ_{max} on low-N and low-P media

Ranks are computed on the mean of 5 replicate kinetics for each evolved strain, performed on 4 days. Shapes and colors of the points code for the different evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$.

1.14 APPENDIX E – N* ~ P* RELATIONPHIP

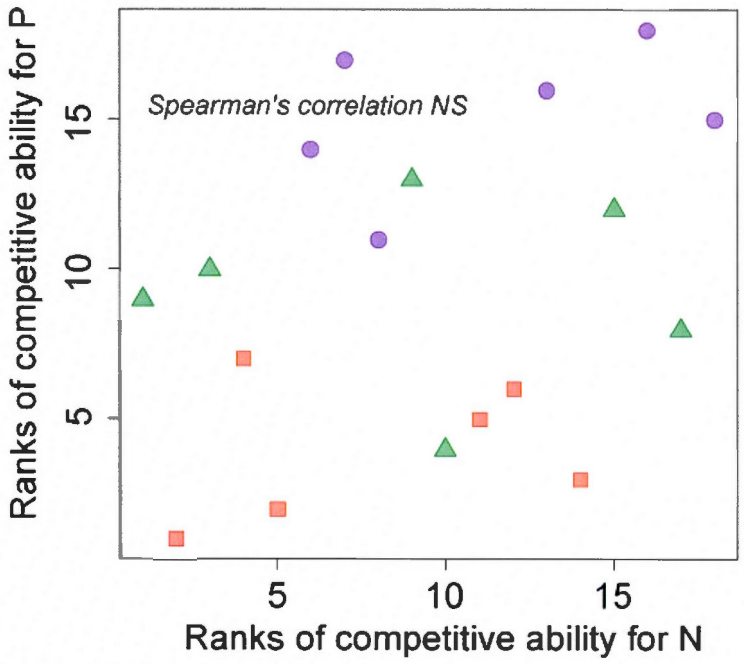

Fig. E Relationship between maximum per capita growth on low-N and low-P media

Ranks are computed on the mean of 5 replicate kinetics for each evolved strain, performed on 4 days. Shapes and colors of the points code for the different evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$.

1.15 APPENDIX F – CELL SIZE DISTRIBUTION

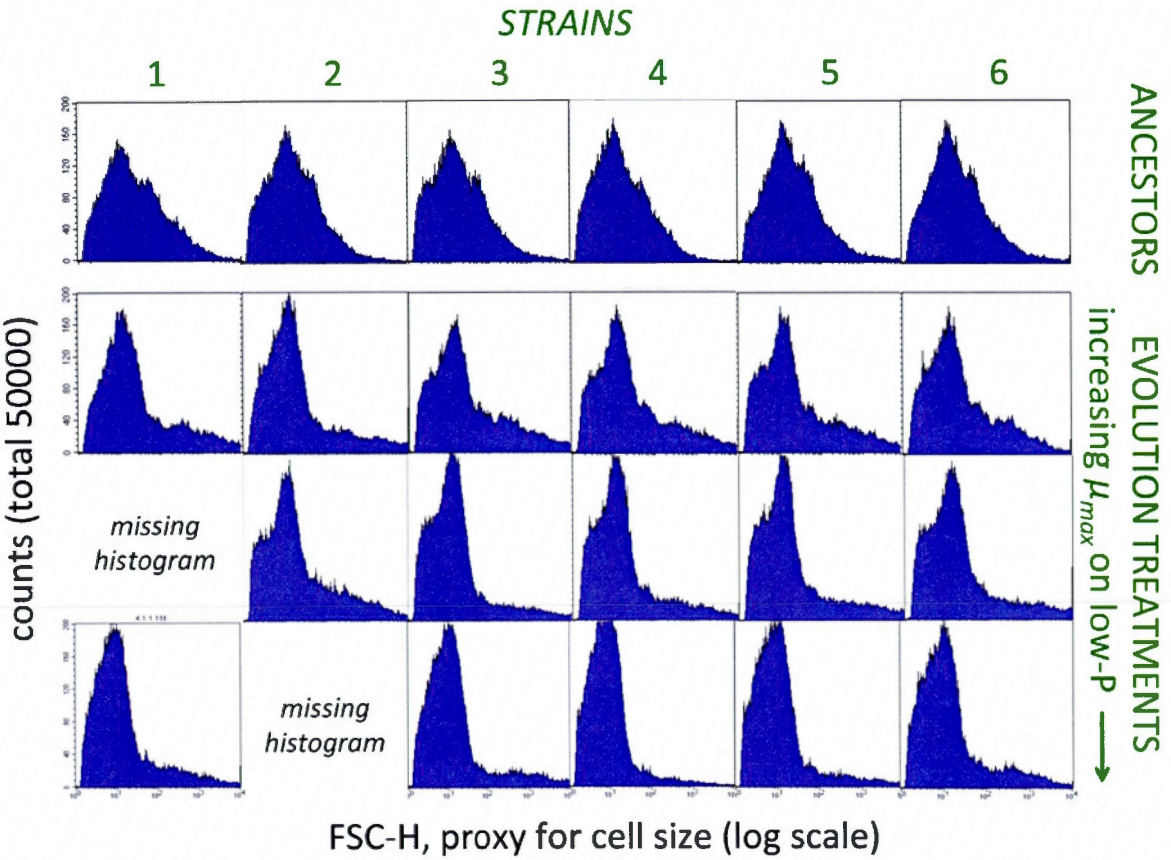

Fig. F Histograms of cell sizes

Cell size is approximated by the FSC-H parameter measured by flow cytometry on 50 000 events by population. Each histogram is an example of one population over the 6 population replicates measured by ancestor and evolved strains

1.16 APPENDIX G – N*/P* ~ CELL SIZE RELATIONSHIP

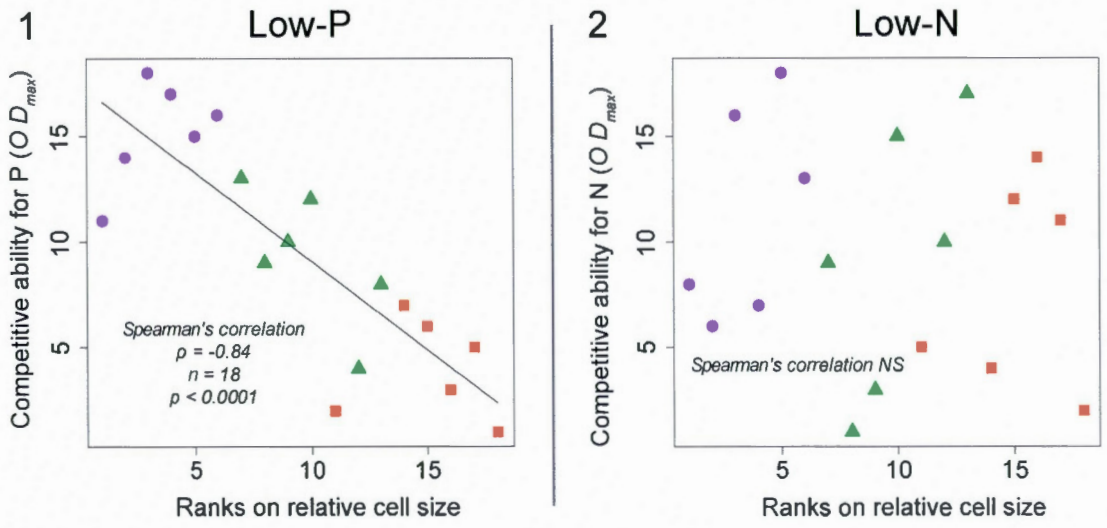

Fig. G Relationship between ranks of competitive abilities for P (panel 1) or N (panel 2) and of average relative cell size

The relative cell size is approximated with the geometric mean of the FSC-H parameter distribution in the population, measured by flow cytometry over 50 000 events. Ranks are computed on the mean of the replicate measures for each evolved strain (5 replicate populations for the measure of the μ_{max} and 6 replicate populations for the screaning of population cell sizes). Point shapes and colors code for the evolution treatments: red squares are for $VT10^{-2}$, green triangle for $VT10^{-3}$ are and purple circles for $VT10^{-4}$.

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CHAPITRE 2
INTERACTIONS SPATIALES ENTRE RESSOURCES INORGANIQUES ET DYNAMIQUE PLANTE-HERBIVORE

2.1 TITRE DE L'ARTICLE

Le paradoxe de l'enrichissement en métaécosystèmes

2.2 RÉSUMÉ

Le « paradoxe de l'enrichissement » a été presque exclusivement étudié dans le cadre des communautés ou des méta-communautés, sans dynamique explicite des nutriments inorganiques. Pourtant le recyclage local de matière venant d'écosystèmes enrichis pourrait aussi affecter la stabilité des écosystèmes qui y sont connectés.

Ici nous étudions l'effet de flux spatiaux de nutriments inorganiques, détritus, d'un producteur primaire et d'un herbivore, combinés à des variations de l'enrichissement régional, sur la stabilité d'un modèle de métaécosystème. Nous considérons aussi bien des enrichissements spatialement homogènes qu'hétérogènes.

Nous trouvons que les flux spatiaux de nutriments inorganiques ou de détritus sont déstabilisants, alors que les flux spatiaux de producteurs ou d'herbivores sont soit neutres, soit stabilisants. L'effet des flux spatiaux de détritus sur la stabilité est particulièrement ténu. Notre étude révèle que l'hétérogénéité environnementale ne suffit plus à stabiliser des écosystèmes très connectés lorsque la dynamique des nutriments est explicite. Nous trouvons aussi qu'un taux intermédiaire de dispersion de l'herbivore peut conduire à des équilibres multiples dans les métaécosystèmes fortement enrichis. Une stabilisation peut alors émerger d'un contrôle de la croissance du producteur par l'herbivore qui permet un stockage de l'excédent d'enrichissement sous une forme inorganique, un mécanisme encore jamais documenté.

Pour récapituler, un enrichissement local pourra être stabilisé si les flux spatiaux sont suffisamment intenses pour redistribuer efficacement l'excès d'enrichissement vers des écosystèmes moins fertiles. Cependant, une déstabilisation résultant d'un fort enrichissement régional ne pourra être jugulé que par des taux intermédiaires de dispersion des herbivores.

Cet article intitulé « The paradox of enrichment in metaecosystems » a été co-rédigé par moi-même, mes directeurs de thèse Dominique Gravel et Nicolas Mouquet, et les chercheurs Elsa Canard, Frédéric Guichard et Céline Hauzy. Le manuscrit a été accepté pour publication en août 2014 dans la revue *The American Naturalist*.

En tant que première auteure, j'ai réalisé la recherche bibliographique, la programmation du modèle et l'analyse des résultats ainsi que l'essentiel de la rédaction. Mes directeurs Dominique Gravel, dernier auteur, et Nicolas Mouquet, second auteur, ont fourni l'idée originale et le choix du modèle (d'après Gravel et al. 2010), aidé au choix des figures et à l'examen des résultats, et participé à la rédaction du manuscrit. Elsa Canard, Frédéric Guichard et Céline Hauzy, respectivement 3ème, 4ème et 5ème auteurs ont participé à la rédaction du manuscrit.

J'ai présenté un poster exposant les principaux résultats de cette étude à la 97ème conférence annuelle de la Société Américaine d'Écologie (ESA) en août 2012, à Portland. J'ai aussi donné une présentation des résultats lors du séminaire de Modélisation en Écologie Évolutive de Montpellier en mai 2012.

2.3 TITLE

The paradox of enrichment in metaecosystems

2.4 ABSTRACT

The "paradox of enrichment" has been studied almost exclusively within communities or metacommunities, without explicit nutrient dynamics. Yet, local recycling of materials from enriched ecosystems may affect the stability of connected ecosystems. Here we study the effect of nutrient, detritus, producer, and consumer spatial flows, combined with changes in regional enrichment, on the stability of a metaecosystem model. We considered both spatially homogeneous and heterogeneous enrichment. We found that nutrient and detritus spatial flows are destabilizing, whereas producer or consumer spatial flows are either neutral or stabilizing. We noticed that detritus spatial flows have only a weak impact on stability. Our study reveals that heterogeneity no longer stabilizes well-connected systems when accounting for explicit representation of nutrient dynamics. We also found that intermediate consumer diffusion could lead to multiple equilibria in strongly enriched metaecosystems. Stability can emerge from a top-down control allowing the storage of materials into inorganic form, a mechanism never documented before. In conclusion, local enrichment can be stabilized if spatial flows are strong enough to efficiently redistribute the local excess of enrichment to unfertile ecosystems. However, high regional enrichment can only be dampened by intermediate consumer diffusion rates.

2.5 KEYWORDS

Stability, dispersal, spatial heterogeneity, source-sink dynamics, fertility, alternative stable states.

2.6 INTRODUCTION

Rosenzweig (1971) defined the "paradox of enrichment" as the destabilization of consumer-resource dynamics observed after resource enrichment. This phenomenon has been recently understood as belonging to "the principle of energy flux", a general response of consumer-resource dynamics to an increase in the nutrient input relative to output balanced by the consumer (Rip and McCann 2011). Among other causes, resource enrichment increases this balance (referred to as "the relative energy flux" by Rip and McCann 2011) and hence the consumer: resource biomass ratio (McAllister *et al.* 1972). The lag between consumer and resource growth makes these "top-heavy" consumer-resource interactions less stable, and prone to oscillations. Then over-production of the resource alternates with over-compensation of the consumer (May et al. 1974, Murdoch *et al.* 2003). Enrichment-driven instabilities (*sensu* Otto *et al.* 2007) have been observed in experimental microcosms (Luckinbill 1973, Fussmann *et al.* 2000, Becks *et al.* 2005, Van der Stap *et al.* 2009), controlled field experiments (Bjørnsen *et al.* 1988, Lecomte *et al.* 2004, Meyer *et al.* 2012) and even in nature (*i.e.* some herbivorous insect outbreaks have been linked to nitrogen enrichment: Myers and Post 1981, Brunsting and Heil 1985).

Though good examples exist, many experimental tests of these enrichment–driven instabilities are not consistent with the "paradox of enrichment" (e.g. Murdoch *et al.* 1998, Daugherty 2011). Moreover field evidence for increased instability related to nutrient enrichments is scarce despite widespread ecosystem enrichments (Krupa 2003, Duce *et al.* 2008, Elser *et al.* 2009). Several mechanisms have been invoked to explain why this destabilization might not happen in complex ecosystems (Roy and Chattopadhyay 2007 for a review). These mechanisms include factors relative to the resource species that limit the nutrient input to the consumer, such as unpalatability, lower quality, inducible defenses, refuges or alternative resources (Genkai-Kato and Yamamura 1999, Urabe and Sterner 1996, Van Baalen *et al.* 2001, Vos *et al.* 2004, Verschoor *et al.* 2004). Stability also emerges from factors that increase nutrient output from the consumer, such as cannibalism (Chakraborty and Chattopadhyay 2011), parasitism (Hilker and Schmitz 2008), interference (Auger *et al.* 2006, Cabrera 2011) or trophic complexity (Trzcinski 2005).

Spatial structure has also been shown to be an important stabilizing factor of consumer-resource interactions (Murdoch *et al.* 2003, Briggs and Hoopes 2004, Amarasekare 2008). Indeed, spatial structure increases consumer-resource persistence by creating permanent or temporary refuges for the resource (Huffaker 1958, Ellner *et al.* 2001, Neubert *et al.* 2002, Brockhust *et al.* 2006, Hauzy *et al.* 2010b). Local extinctions can also be prevented by dispersal from other patches (Holyoak and Lawler 1996), and populations in unfavorable ecosystems ("sinks") can be maintained by immigration from more favorable "source" ecosystems (Amezcua and Holyoak 2000, Casini *et al.* 2012). Briggs and Hoopes (2004) identified three mechanisms by which random dispersal stabilizes consumer-resource interactions in metacommunity models. (1) Oscillations of regional abundances can be dampened by intermediate dispersal that leads to spatial asynchrony in local abundances (de Roos *et al.* 1991, Jansen 1995, 2001, Maser *et al.* 2007). (2) In heterogeneous landscapes, limited dispersal can also be stabilizing if immigration is weaker when local densities peak. Dispersal is then driving an indirect negative density-dependence, which dampens local oscillations (Klepac *et al.* 2007, Sugie and Saito 2012). (3) Dispersal can also stabilize dynamics of spatial predator-prey systems with non-linear functional responses. If dispersal promotes a spatially heterogeneous distribution of the resource, the predator will be, on average across the landscape less efficient at exploiting its resource compared to one with a homogeneous distribution (e.g. de Roos *et al.* 1998). Such a reduction of the relative input to the predator is stabilizing (Rip and McCann 2011). In this case, dispersal in metacommunities can lead to multiple equilibria that have either symmetric or asymmetric spatial distributions of population densities depending on initial conditions, the latter being more stable (Jansen 1995, 2001; Hauzy *et al.* 2010a).

All these studies argue for a stabilizing effect of spatial dynamics, but none of them integrates the spatial dynamics of inorganic nutrients. However, an increasing number of studies have emphasized that nutrient enrichment occurs naturally due to inorganic and organic spatial flows (Polis *et al.* 1997, Loreau *et al.* 2003, Massol *et al.* 2011). These spatial flows have now been well-documented. They include migration roads linking

distant ecosystems (Jefferies *et al.* 2004, Varpe *et al.* 2005), nutrient transfers by whales linking euphotic and deep zones in oceans (Lavery *et al.* 2010, Roman and McCarthy 2010), detritus and organisms linking lakes and surrounding landscapes (Gratton *et al.* 2008, Paetzold *et al.* 2011, Rösel *et al.* 2012), or sea-to-land transport of nutrients by seabirds (Fukami *et al.* 2006, Maron *et al.* 2006). In addition, local spots of enrichment due to human activities are widespread (Halpern *et al.* 2007). Spatial flows from these spots may affect the stability of neighboring ecosystems. Inorganic nutrient flows have been shown to potentially destabilize consumer-resource interactions (Marleau *et al.* 2010, Suzuki and Yoshida 2012). But it is also likely that local recycling of organic matter brought by dispersal from enriched ecosystems, will impact the fertility of ecosystems that receive it. Recycling plays a crucial role in the primary productivity of many ecosystems (Simon *et al.* 2002, Van der Heijden *et al.* 2008). Therefore, the combination of spatial flows with local recycling might play an essential role in consumer-resource regional dynamics under enrichment.

Spatial exchanges of nutrients and organic material are formalized in the concept of metaecosystem, defined as a set of local ecosystems linked by spatial flows of inorganic nutrients, detritus and/or organisms (Loreau *et al.* 2003, Massol *et al.* 2011). By integrating explicitly the dynamics of inorganic nutrients with recycling and spatial flows, the metaecosystem framework efficiently addresses questions related to feedbacks between species interactions and ecosystem processes. The metaecosystem study of Marleau and colleagues (2010), for instance, has shown how nutrient flows can affect the response of simple ecosystems to enrichment across homogeneous landscapes. Two natural extensions are required to draw up a comprehensive analysis of the consequences of dispersal on enrichment-driven instabilities. First, the effect of spatial flows of organic compartments (producer, consumer and detritus) has to be investigated. Indeed, organisms and detritus spatial flows may affect ecosystem stability by changing local nutrient supply through mineralization (Wolf *et al.* 2013). Second, heterogeneity in the distribution of enrichment may also have important impacts on stability. Spatial heterogeneity generates spatial flows,

with local enrichment inevitably corresponding to impoverishment elsewhere (Loreau *et al.* 2003, Gravel *et al.* 2010a and 2010b).

In this study we revisit the "paradox of enrichment" within the perspective of metaecosystems. We use a simple two-ecosystem model integrating space, trophic interactions, and explicit nutrient dynamics. Our metaecosystem can represent the coupling between pelagic and benthic areas (Schindler and Scheuerell 2002), or between lakes (Griffiths *et al.* 2013). Aquatic systems are commonly impacted by enrichment (Halpern *et al.* 2007). They can be spatially heterogeneous because of physical structures such as small bays or abrupt changes in floor depth, or because of environmental gradients (*e.g.* light). Moreover, recycling plays an important role in these systems (Kiørboe 2001) and often couples different ecosystems (Roman and McCarthy 2010, Ryabov and Blasius 2011). We analyze how metaecosystem stability is affected by nutrient enrichment and dispersal of the different ecosystem compartments. This study addresses two main questions: (i) how do the spatial flows of specific ecosystem compartments (nutrient, *detritus, and* organisms) act on the destabilizing effect of enrichment; and (ii) what is the impact of spatial heterogeneity of ecosystem enrichment on stability? The metaecosystem framework reveals that the effects of diffusion on local dynamics depend crucially on the nature (alive *versus* inert) of the spatial flows. Moreover, we show that heterogeneity is not stabilizing for well-connected ecosystems, and that consumer spatial flows can lead to a specific stabilizing effect by maintaining a part of the enrichment into inorganic form.

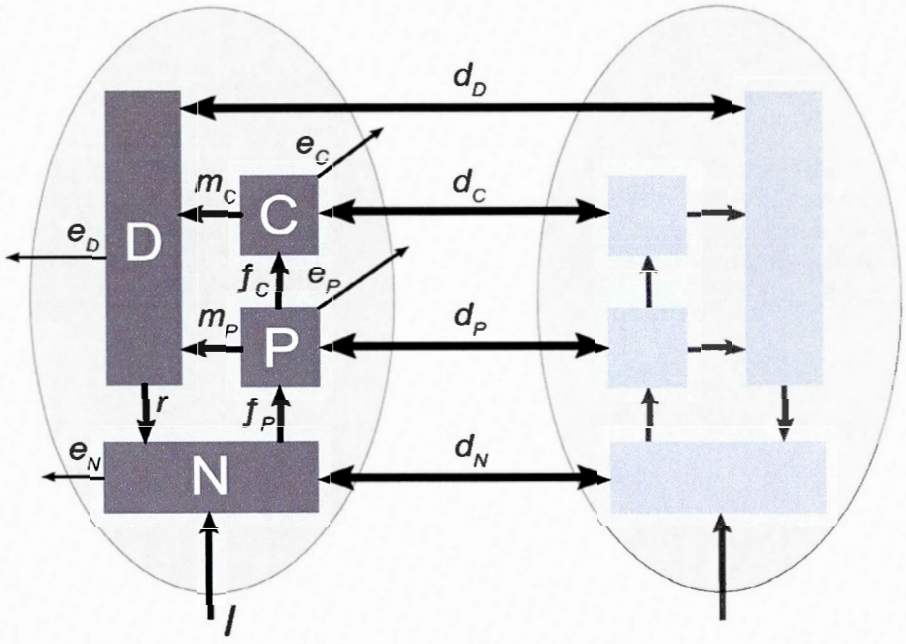

Fig. 1 Metaecosystem model (adapted from Gravel *et al.* 2010a)
In each of the two ecosystems the primary producer P consumes the inorganic nutrient N and is consumed by the primary consumer C. P and C produce detritus D at respective rates m_P and m_C, mineralized into N at a rate r. The functional responses of the organisms, f_P and f_C take a Holling type II form. N receives constant input I from the outside. Each compartment loses material at constant output rates e_N, e_P, e_C, e_D. The ecosystems are connected by spatial flows between their homologous compartments N, P, C, D, according to constant diffusion rates d_N, d_P, d_C, and d_D, respectively.

2.7 METHODS

2.7.1 The metaecosystem model

We considered two open ecosystems inhabited by a producer-consumer species pair where organic matter is locally recycled (after Gravel *et al.* 2010a). The ecosystems are

connected by passive spatial flows of organisms and matter, thereby forming a metaecosystem (fig. 1). We used a compartment model in which the dynamics of the densities in ecosystem i ($i \in \{1,2\}$) are given by the following differential equations:

$$\frac{dN_i}{dt} = I_i - e_N N_i + rD_i - P_i f_P(N_i) + d_N \Delta_{N_i}$$

$$\frac{dP_i}{dt} = P_i f_P(N_i) - (m_P + e_P)P_i - C_i f_C(P_i) + d_P \Delta_{P_i} \quad [1]$$

$$\frac{dC_i}{dt} = C_i f_C(P_i) - (m_C + e_C)C_i + d_C \Delta_{C_i}$$

$$\frac{dD_i}{dt} = m_P P_i + m_C C_i - (r + e_D)D_i + d_D \Delta_{D_i}$$

In each local ecosystem, the (primary) producer P consumes the single limiting inorganic nutrient N and is grazed by the consumer C. The metabolism and the mortality of the producer and consumer generate detritus D at rates m_P and m_C respectively. Detritus is mineralized into inorganic nutrient N at a rate r. We considered Holling type II functional responses (f_P and f_C, Holling 1959) for both the producer and the consumer, following the Rosenzweig's predator-prey model (1971): $aX/(1 + bX)$ where a is the attack rate on resource X (either N or P) and b a parameter taking into the account physical limitations of the organisms (*e.g.* time required to metabolically transform a resource into new matter, satiety of the consumer, *etc.*).

Each ecosystem i is open to external inputs and outputs. Inorganic nutrients are supplied locally with a fixed input flow I_i. Matter can be lost from each local compartment N_i, P_i, C_i, D_i, at rates e_N, e_P, e_C and, e_D respectively (*e.g.*: consumption by other species, which is not considered here, sedimentation or volatilization). Ecosystems are connected by spatial flows between homologous compartments (fig. 1). We assume passive spatial flows, with a net movement of matter from high to low concentration compartments occurring at constant diffusion rates d_X for a given compartment X, with $\Delta_{X_1} = X_2 - X_1$ in ecosystem 1 and the opposite for ecosystem 2. We use input of inorganic nutrients I as a proxy for fertility (keeping e_N constant) and the diffusion rates as indicators of metaecosystem

connectivity. Units are expressed in standard dimensions MLT: Mass, Length, Time (see table 1).

Table 1: Summary of the abbreviations used in the text

Symbol	Definition	Unit	Values
N, P, C, D	Densities of the inorganic nutrient, producer, consumer and detritus compartments	$M.L^{-2}$	-
I_i	Inorganic nutrient flow in ecosystem i	$M.L^{-2}.T^{-1}$	-
e_N, e_P, e_C, e_D	Output rates of the different compartments	T^{-1}	0.1
r	Mineralization rate	T^{-1}	0.5
a_P, a_C	Producer and consumer consumption rates	$T^{-1}.(M.L^{-2})^{-1}$	0.5
b_P, b_C	Producer and consumer saturation parameters: $b = a * h$ with h the handling time.	$(M.L^{-2})^{-1}$	0.5
m_P, m_C	Producer and consumer mortality rates	T^{-1}	0.5
d_N, d_P, d_C, d_D	Diffusion rates of the different compartments	T^{-1}	0
f_P, f_C	Functional responses of the producer and the consumer	T^{-1}	-
ΔI	Environmental heterogeneity ($\Delta I = I_1 - I_2$)	$M.L^{-2}$	$\{0, 0.5\}$
λ_{max}	Real part of the dominant eigenvalue of Jacobian matrix	T^{-1}	-

2.7.2 Analysis

We focused on the local stability of the metaecosystem. We analyzed the effect of fertility and diffusion rates on the real part of the dominant eigenvalue, λ_{max}, obtained numerically from equation [1] linearized at each equilibrium. We first determined the possible equilibria of the system, *i.e.* the set of positive densities that are reached when the growth rates of all the compartments are simultaneously set to zero. We then computed the Jacobian matrix and its eigenvalues. The absolute value of the real part of the dominant eigenvalue ($|\lambda_{max}|$) is a measure of resilience (May 1973) and the equilibrium is stable when λ_{max} is negative. The analytical solutions of this system of eight equations were intractable and we consequently used numerical analysis with a solver from R 2.10.1 (package *rootSolve*, Soetaert and Herman 2009) to find the equilibria. To get an overview of the

system behavior, we plotted the stability isocline ($\lambda_{max} = 0$) for a given parameter space (online Appendix A for more details).

As a preliminary analysis we first studied the stability of a local ecosystem without spatial flows ($d_N = d_P = d_C = d_D = 0$). The effects of the 12 parameters on stability were consistent with the principle of energy flux (online Appendix A). To address our questions, we then restricted our analysis of the metaecosystem stability to changes of fertility and diffusion rates, keeping the same set of values for other parameters (see table 1). We characterized the effect of each spatial flow independently (either N, P, C or D), and in combination, on the critical fertility level inducing destabilization. These scenarios of connectivity represent extreme cases where spatial flows can be either strongly unbalanced or equivalent. The spatial flows may be unbalanced if the factors involved in diffusion rates act differently on the different compartments. For instance, the intensity of mixing between pelagic and benthic areas may differ according to the specific density of the compartment components (Herbert 1999). Moreover, the one-flow scenarios enabled us to characterize the particular effects resulting from the diffusion of each ecosystem compartment. We explored a range of diffusion rates from low to high compared to the rate of local dynamics. We started with the simplest case of a homogenous enrichment and then introduced spatial heterogeneity of the enrichment, ΔI, defined as the difference between local fertilities ($\Delta I = I_1 + I_2$). We present here the case for $\Delta I = 0$ (*e.g.*: atmospheric deposition over all ecosystems, Carpenter *et al.* 1998, Krupa 2003, Greaver *et al.* 2012) and for $\Delta I = 0.5$ (*e.g.*: localized enrichment of a lake in a watershed, Fisher *et al.* 2000, Carpenter 2005). We kept ΔI constant while varying the regional fertility of the metaecosystem ($(I_1 + I_2)/2$), to separate the effects of heterogeneity from those of enrichment. We expected environmental heterogeneity to influence metaecosystem stability through source-sink dynamics (Gravel *et al.* 2010a).

2.8 RESULTS

We first analyzed the effect of a single spatial flow (d_N, d_P, d_C, or d_D) while setting

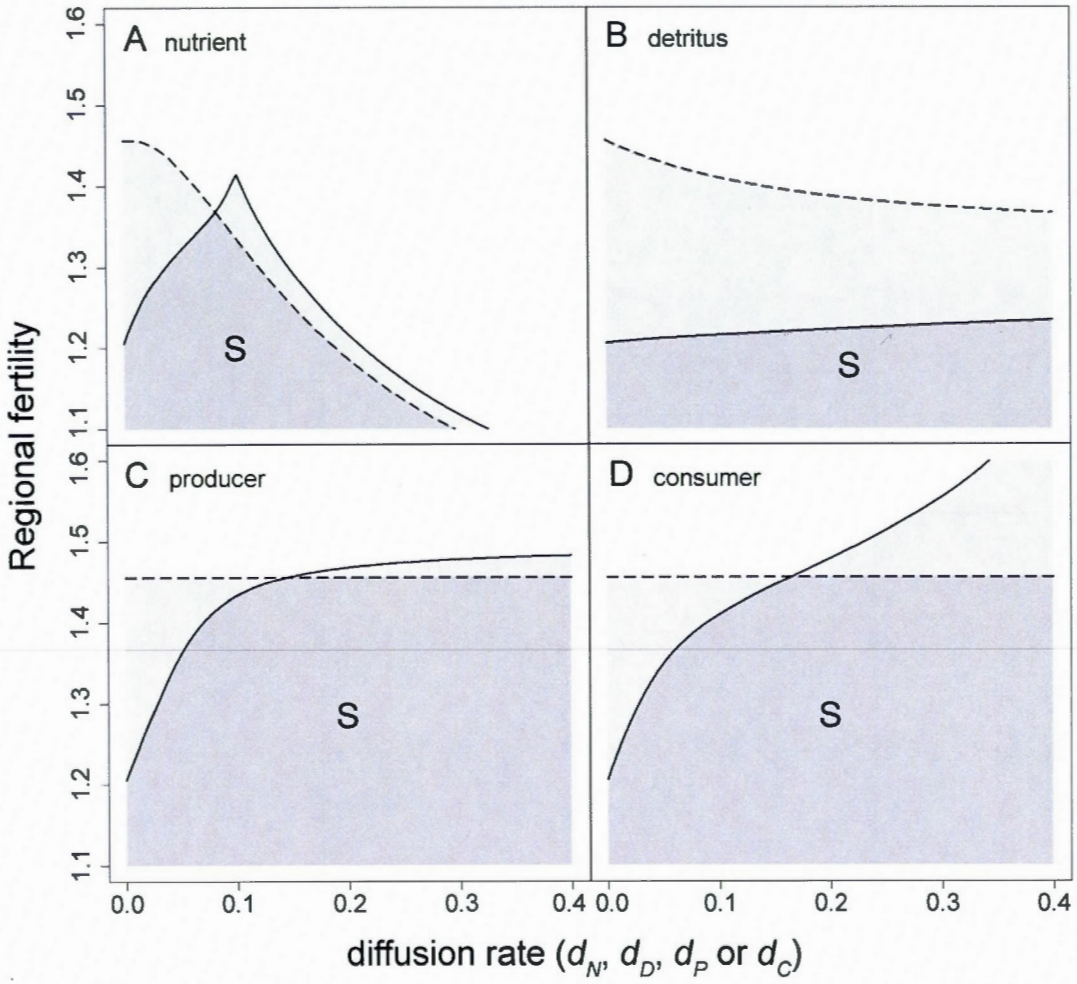

Fig. 2 Stability with a single spatial flow

Each panel represents the stability isoclines under changes of one diffusion rate (the others set to zero), either d_N, d_D, d_P, or d_C for panels *A*, *B*, *C* and *D* respectively, *versus* regional fertility of the metaecosystem ($(I_1 + I_2)/2$). The stability isoclines are the pairs of parameter values for which λmax equals zero, either in a homogenous metaecosystem with $\Delta I = 0$ (dashed lines) or in a heterogeneous metaecosystem with $\Delta I = 0.5$ (solid lines). Stability isoclines delimit the grey parameter space (noted S) where λmax is negative and thereby the equilibrium is stable. See Table 1 for symbols and other parameter values, and online appendix B*3* for supplementary details regarding panel *B*.

the others to zero (fig. 2). In a homogenous environment (*i.e.* ecosystems with similar local fertilities; $I_1 = I_2$), we found that ecosystems are less robust to enrichment when they are connected by spatial flows of detritus or nutrient, than isolated ecosystems (figs. 2*A* and 2*B*, dashed lines). In contrast, spatial flows of producers and consumers do not impact ecosystem stability (figs. 2*C* and 2*D*, dashed lines).

Spatial heterogeneity of fertility ($I_1 \neq I_2$) destabilizes at low diffusion rates and stabilizes at high diffusion rates (fig. 2, solid lines cross dashed lines), except with detritus spatial flows (fig 2B). Under high diffusion rates, we observed the same destabilizing effect

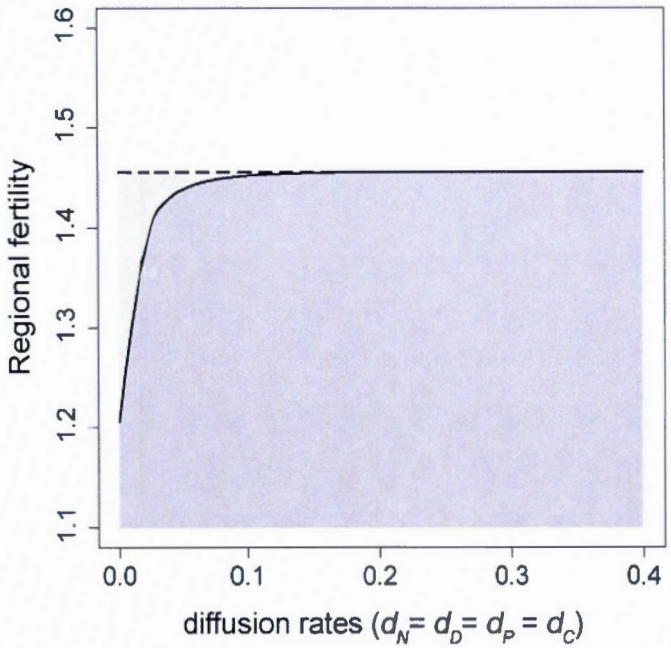

Fig. 3 Multiple spatial flows

Stability isoclines (see fig. 2 for the definition) under increasing diffusion rates for all compartments *versus* metaecosystem regional fertility ($(I_1 + I_2)/2$). Stability isoclines delimit the grey area where the equilibrium is stable for homogenous (dashed lines, $\Delta I = 0$) and heterogeneous (solid lines, $\Delta I = 0.5$) metaecosystems. See Table 1 for other parameter values.

of nutrient spatial flows, and no effect of producer spatial flows, as found for homogenous metaecosystems. Interestingly, high consumer spatial flows seem to produce an additional stabilizing effect in heterogeneous metaecosystems.

The metaecosystem is overall more stable at low diffusion rates when all compartments are diffusing compared to single spatial flows (solid lines, fig. 2, 3). However, in contrast to single spatial flows, heterogeneity does not have a stabilizing effect at high diffusion rates. Isoclines of homogeneous and heterogeneous metaecosystems converge to the same fertility threshold observed in isolated ecosystems (fig. 3).

We found that consumer diffusion can generate multiple equilibria when intermediate diffusion rates are combined with high values of regional fertility (fig. 4). In a homogenous metaecosystem, we found up to three non-trivial equilibria, corresponding to two very different biomass distributions. The first one is the most intuitive: the two ecosystems are symmetric (*i.e.* with identical densities) and dynamics oscillate in complete phase synchrony (figs. 4*C*, 4*E*). The second is an asymmetric source-sink structure (figs. 4*D* and 4*F*), which can be a stable point for intermediate consumer diffusion rates ('Mix.' zone in fig. 4*A*, orange line in fig. *4B*). An initial perturbation allows the producer of one of the two ecosystems to exploit its abundant resource. This ecosystem produces numerous consumers and therefore becomes a 'realized source' (*sensu* Gravel *et al.* 2010a), which means here a net exporter. The consumers are exported to the second ecosystem, where they prevent the growth of the producer despite abundant inorganic resources. Subsequently, the organic matter brought by the consumers is mainly stored in the nutrient compartment of the second ecosystem, which becomes a 'realized sink' (a net importer). This results in a stabilizing spatial asymmetry in ecosystem control (top-down *versus* bottom-up controlled ecosystems). Hence, consumer spatial flows allow a regional stabilization for a set of intermediate diffusion rates, even when enrichment reaches high levels. This area of possible stabilization expands with the heterogeneity of enrichment distribution, because asymmetry in fertility induces source-sink dynamics that facilitates the set up of asymmetry in ecosystem control (online Appendix B1).

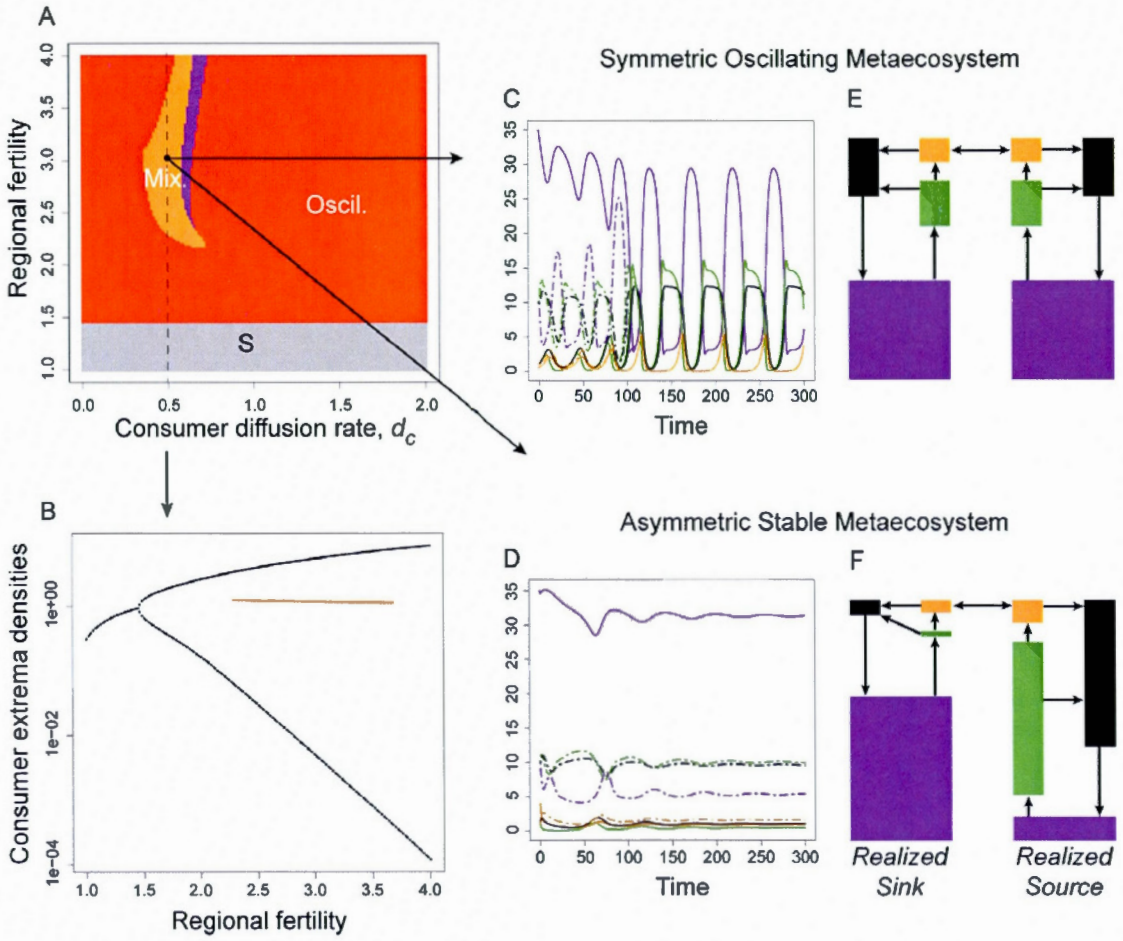

Fig. 4 Multiple equilibria with intermediate consumer diffusion rates and high enrichment levels in homogeneous metaecosystems

A, Areas of stability for an extended parameter space with regard to fig. 2*D* (d_C ranges from 0 to 2 and regional fertility from 1 to 4), for the homogenous case, with $\Delta I = 0$ (see online appendix C for the heterogeneous case). Grey area (*S*): stable equilibria ($\lambda max<0$); red area (*Oscil.*): unstable equilibria ($\lambda max>0$); orange and purple areas have multiple equilibria, either all unstable (purple area) or one unstable and 2 stable (Mix. orange area). *B,* bifurcation diagram of consumer extreme densities (spatial average) according to regional fertility, for the consumer diffusion rate $d_C = 0.5$ (vertical line on panel *A*). The orange equilibria are stable (maximum = minimum), the black unstable. Panels {*C, E*} and {*D, F*} illustrate the two equilibria types for the pair of parameters {$d_C = 0.5$, regional fertility=3}. Panels *C* and *D* show the dynamics of all the compartments. Panels *E* and *F* show the relative densities of the different compartments (heights proportional to the temporal mean density at equilibrium). Between the two cases, initial densities vary only for the consumer of ecosystem 2: C_2=0.5 in {C, E}, C_2=4 in {D, F}. See Table 1 for symbols and other parameter values.

2.9 DISCUSSION

The metaecosystem framework makes three new predictions regarding the stability of ecosystems under enrichment. First, the nature of the compartment diffusing between ecosystems determines whether diffusion enhances enrichment-induced instabilities or not. Spatial flows of "non-living" compartments (nutrients or detritus) are destabilizing whereas spatial flows of "living" compartments (producer or consumer) are either neutral or stabilizing. Second, spatial heterogeneity in supply rates is no longer stabilizing in well-connected ecosystems, and can even be destabilizing when diffusion is restricted to detritus. Third, intermediate spatial flows of consumers can switch dynamics from oscillating to stable even under high enrichment. We discuss below the underlying mechanisms driving these three predictions, the robustness of our results and future directions.

2.9.1 Living versus non-living spatial flows

We found neutral *versus* negative effects on stability of living *versus* non-living spatial flows, respectively. We attribute this difference to their opposite effect on spatial synchrony (co-variation between time series, Liebhold *et al.* 2004). Indeed, spatial flows of living organisms lead to in-phase synchrony (positive co-variation), whereas spatial flows of non-living matter lead to asynchrony (see online appendix B2 for examples). Spatial synchrony usually has negative effects on ecosystem stability by increasing the global extinction risk, or reducing the effect of dispersal (Earn *et al.* 2000). In homogenous metaecosystems, we observe perfect in-phase synchrony even for very low diffusion rates of living compartments ("phase locking", Jansen 1999, Goldwyn and Hastings 2008), which cancels any potential stabilization via source-sink dynamics (Vogwill *et al.* 2009). However, if heterogeneity prevents perfect synchrony, diffusion can synchronize the dynamics while they are stabilized by other mechanisms (like in Abbott 2011). In contrast, spatial flows of non-living compartments (inorganic nutrients and detritus) promote asynchrony, and thereby sustain enrichment-induced instabilities in each ecosystem

alternatively. Spatial asynchrony makes regional densities less variable (de Roos *et al.* 1991, Wilson *et al.* 1993, Briggs and Hoopes 2004), but accentuate parallel local instabilities (Maser et al. 2007). We also observed this destabilization, as other recent metaecosystem studies (Marleau *et al.* 2010, Suzuki and Yoshida 2012) and tri-trophic connected systems (Koelle and Vandermeer 2005). This asynchrony stems from the restriction of diffusion to basal resources, which boiled the system down to oscillators coupled by resource competition (Vandermeer 2004).

In addition to being consistent with previous synchrony – stability studies, our analysis highlights the link between spatial synchrony and the diffusion of the different compartments of ecosystems. What matters is whether the compartment is donor or recipient controlled. If the compartment actively consumes a resource, diffusion of this compartment will be fundamentally homogenizing. The consumption activity buffers the spatial differences of resource densities, while diffusion buffers spatial differences of consuming species densities. This crucial role of consumption for the process of homogenization and spatial synchrony has also been reported in an experimental algal-rotifer metacommunity (Vasseur and Fox 2009). In contrast, spatial flows of inert matter (detritus or inorganic nutrients) will increase spatial differences in densities of all compartments by fuelling both resource and growth of organisms in one ecosystem at the expense of the other. Hence it desynchronizes the dynamics and produces punctual over-production in each ecosystem.

We noticed also a much weaker destabilization with detritus than with nutrient diffusion. The delay of mineralization that transforms detritus into available resource lessens the impact of detritus diffusion on regional stability. Detritus act as a storage compartment whose inertia temporarily removes matter from the enrichment destabilization process. Parameters favoring the accumulation of detritus (e.g. low recycling, high mortality rates) are therefore stabilizing (online appendix B*3*). The effect of detritus diffusion on stability saturates quickly because recycling constitutes a bottleneck for the energy flux into the system. This suggests that, even if detritus spatial flows constitute substantial subsidies to some webs (Shen *et al.* 2011), their increased transfer between

ecosystems (e.g. with storms) should not have a strong impact on stability. Note that this result probably does not hold for detritivorous-based metaecosystems, where organisms feeding on detritus bypass the bottleneck of recycling, changing the storage status of detritus (Edwards 2001, Cross *et al.* 2006).

2.9.2 Non-stabilizing Heterogeneity

With only one compartment diffusing between ecosystems (fig. 2), heterogeneity of enrichment is destabilizing at low diffusion and stabilizing at high diffusion, like in metacommunities (Hauzy *et al.* 2013). At low diffusion, the oscillations of the most fertile ecosystem are spread to the stable less fertile one, like environmental noise (Poggiale *et al.* 2008). Past a certain intensity of diffusion, heterogeneous metaecosystems are more resistant to enrichment than homogenous ones (fig. 2*A*, 2*C* and 2*D*). The stabilizing effect of heterogeneity emerges from the non-linearity of species dynamics. Spatial heterogeneity reduces the regional productivity due to inefficient consumption by the producer in the most fertile patch (online appendix B*4*). This mechanism, originating from the saturating functional response, belongs to what was previously reported as *non-linear averaging* (*sensu* Briggs and Hoopes 2004, Nisbet *et al.* 1998, Hauzy *et al.* 2013). The more saturating the producer functional response, the larger the stabilization (Online appendix C).

What novel insight our metaecosystem framework adds is that this positive effect of heterogeneity can be decreased, or even cancelled by diffusion (fig. 3). When all compartments are diffusing, source-sink dynamics can be so strong that even inorganic nutrient availability is homogenized, despite the fixed differences of external inputs between ecosystems. Subsequently heterogeneity and its stabilizing property disappear. As a side effect, homogenization increases the regional productivity. These effects of homogenization cannot be expressed in metacommunities where heterogeneity in fertility is modeled by carrying capacities (Hauzy *et al.* 2013), because the stabilizing effect of heterogeneity is independent from diffusion. Similarly, stabilization can be maintained in our metaecosystem if we add spatial heterogeneity in demographic parameters independent

from nutrient supply (Online Appendix C). The explicit representation of nutrient dynamics in metaecosystems reveals that heterogeneity in fertility has to be associated with restricted diffusion (single spatial flows) to produce a stabilizing effect. In addition, if only detritus diffuses, the regional redistribution of the enrichment via source-sink dynamics might be so weak that heterogeneity is destabilizing whatever the diffusion rate (fig. 2*D*, online appendix B*3*). Spatial flows of detritus have neither the homogenizing properties of organisms that actively consume their resource, nor the stabilizing efficiency of nutrient flows, which directly redistribute excess enrichment (because of the time needed for mineralization). Hence, exportation of detritus is unlikely to dampen the oscillations generated by a local enrichment.

2.9.3 Consumer spatial flows and the nutrient storage mechanism

Intermediate consumer spatial flows can stabilize the metaecosystem (figs. 2*D*, 4; online appendix B*1*). Above a threshold rate, consumer emigration relaxes enrichment-induced instability in the most fertile ecosystem. At the same time, heterogeneity maintains asynchrony such that immigration becomes negatively correlated with consumer density in the less fertile ecosystem, which limits the overcompensation inducing oscillations (online appendix D). This indirect negative density-dependence is one of the main mechanisms invoked to explain the stabilizing effect of dispersal (Briggs and Hoopes 2004, Goldwin and Hastings 2009, Howeth and Leibold 2013). When fixed spatial differences maintain asynchrony, immigration can be negatively correlated with local per capita growth rate, reducing the amplitude of oscillations (De Roos *et al.* 1998, Jansen 2001, Neubert *et al.* 2002).

Asynchrony, and subsequent stabilizing negative density-dependence, can also occur in homogenous systems. Intermediate consumer diffusion rates can lead to two different types of equilibria (fig. 4): a symmetric unstable one, and another more stable one, which displays asynchronous dynamics and spatial asymmetry between equilibrium densities. In homogenous metacommunities, this equilibrium displays higher minimal densities than in isolated systems, and the amplitude of oscillations is insensitive to enrichment (Jansen

1995, 2001, and Hauzy *et al.* 2010a). Stabilization can emerge from adaptive movements of the consumer (Abrams and Ruokolainen 2011, Ruokolainen *et al.* 2011). Here we show that asymmetric equilibrium can be stable even with random movements in metaecosystems, through the storage of the extra nutrient input in inorganic form. Diffusion makes one ecosystem become a source of consumers, while in the other, the strong top-down control of immigrate consumers prevents the producer to use its resource. This ecosystem becomes a sink (Loreau *et al.* 2012). For intermediate consumer diffusion rates, the sink ecosystem stores a sufficient part of the enrichment in inorganic form to stabilize the metaecosystem, without increasing the consumer density in the sink such that the spatial flow direction would reverse and the asymmetric structure be cancelled. In this way, the consumer spatial flows limit in the metaecosystem the two drivers of destabilization: overproduction in a top-down controlled sink and overcompensation in a bottom-up controlled source. Hence, both stability and spatial heterogeneity in the distribution of resources can emerge from random movements of consumers when accounting explicitly for nutrient dynamics.

The spatial asymmetry in biomass distribution is analogous to the coupling of fast and slow energy channels by consumers reported for various systems (Rooney *et al.* 2006), such as link between pelagic and benthic areas of lakes by fishes (Schindler and Scheuerell 2002), connected lakes (Griffiths *et al.* 2013) or soil food webs (Moore *et al.* 2004). The two channels display differences in productivities due to traits of organisms (Abrams et al. 2012) or environmental variations (*e.g.* gradients in the water column: Morozov *et al.* 2011), which can produce asynchronous dynamics. The stability results from the rapid foraging of the predator shifting between two energy channels (Rooney *et al.* 2006), or from the preference of the consumer for the slow energy channel (Blanchard *et al.* 2010). We demonstrate that such asymmetric coupled channels can potentially emerge from the consumer movements themselves and induce a stabilizing spatial heterogeneity in top-down regulation. Hence, we hypothesize that if spatially structured ecosystems, like connected lakes, experience homogenous enrichment (*e.g.* atmospheric deposition: Greaver *et al.* 2012) such that algae-grazer dynamics should be destabilized, initial differences

might make dynamics more stable through grazer movements between ecosystems. This mechanism could apply as well to other patchy aquatic habitats like the Everglades where phosphorus is currently massively released through the cutting of trees on islands (Wetzel *et al.* 2009).

2.9.4 Robustness of the results

The effects of diffusion on the stability of enriched ecosystems described here rely on fundamental mechanisms related to synchronization, non-linear averaging, source-sink dynamics and top-down control. The stability boundary we find varies quantitatively with parameter values, but the qualitative effects of diffusion are robust to any change that would not turn off or counteract the underlying mechanisms. As an example, heterogeneity-induced stabilization can disappear if the functional response of the producer is more linear because the effect of non-linear averaging will be lost (Online Appendix C). In contrast, stability can be maintained despite enrichment homogenization through multiple spatial flows if heterogeneity in demographic parameters has an opposite effect on ecosystem productivity than heterogeneity in fertility, because it will induce a non-linear averaging mechanism resistant to diffusion homogenization (Online Appendix C). Finally, the importance of the different mechanisms described depends on the metaecosystem connectivity and the spatial variation of demographic parameters. This shapes the stability of the enriched ecosystems.

2.9.5 Future directions

The study of our very simple model lays foundations to understand the effects of diffusion of the main ecosystem compartments on the stability of ecosystems under enrichment. The results suggest a more moderate role of heterogeneity as a stabilizing factor than previously reported in metacommunities, and stress the importance of metaecosystem configuration (defined as the number, the nature, and the relative intensity of the flows), rather than the net amount of spatial flows between ecosystems, as a predictor of stability. Further research should develop the metaecosystem theory to fully integrate

such topological properties to insure complex ecosystems against the consequences of the so-called "paradox of enrichment".

Our model with random dispersal better fits simple aquatic webs than, for instance, terrestrial webs. Further research should investigate more complex webs and other dispersal strategies (Amarasekare 2007), which are more relevant for terrestrial ecosystems. Next important steps include the integration in metaecosystems of: (i) non-random dispersal of organisms, since foraging behavior could modify the spatial redistribution of resources (Abbas *et al.* 2012, Wolf *et al.* 2013), and (ii) more complex scenarios of detritus pathways. Detritus is only considered here as a delayed resource in a purely autotroph-based web. However, plants or scavengers can also directly use dead organic matter (Wilson and Wolkovich 2011). In addition generalist consumers commonly feed on both autotroph and detritivorous webs where detritus constitute the basal resource (e.g. Davic and Welsh 2004). This might increase in complex ways the effects of detritus spatial flows on productivity (Attayde and Ripa 2008) and thereby on enrichment-induced instabilities.

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2.11 ONLINE APPENDIX A: ANALYSIS DETAILS

2.11.1 Equilibria Calculation

We used Matlab 7.9.0.529 to compute the analytical equilibria of an isolated ecosystem (equations [1] without diffusion terms). The results are detailed in the next section. No solver was able to compute the analytical equilibria with the diffusion coupling, so we used simulation functions in the metaecosystem analysis. We computed the equilibria with the function *stode* in R 2.10.1, (package *rootSolve,* Soetaert and Herman 2009) and computed the eigenvalues of the Jacobian matrix with the function *eigen* (package *base*). For each point, we built a matrix of 2000 sets of initial density values randomly selected from a sequence between 0 and 80, which was the range of densities we can expect with the parameters used. We computed the equilibrium with the function *stode* for all these set of initial values and we retained all feasible equilibria. This procedure was repeated for all points. We also controlled the presence and stability of the multiple equilibria by running the dynamics at some points.

2.11.2 Ecosystem Analysis

Here we present the analytical equilibria of an isolated ecosystem. Then we present the individual effects on ecosystem stability of each parameter (see table 1 for a list of the variables and parameters).

The model defined by Equations [1], without the diffusion terms, has four equilibrium points {N*, P*, C*, D*}. We detailed only the simple solutions:

$$\left\{\frac{I}{e_N}, 0,0,0\right\}, \left\{\frac{1}{\frac{a_P}{m_P + e_P} - b_P}, P^*, 0, D^*\right\}, \left\{N'^*, \frac{1}{\frac{a_C}{m_C + e_C} - b_C}, C'^*, D'^*\right\},$$

$$\left\{N''^*, \frac{1}{\frac{a_C}{m_C + e_C} - b_C}, C''^*, D''^*\right\}$$

The first equilibrium point depicts the situation in which no organisms can maintain. Only the producer can maintain at the second equilibrium point. The coexistence of the producer and the consumer is possible at either the third or the forth equilibrium point. We used ' and '' notations to differentiate complex equilibria of the last two equilibrium points. We noticed that, like in classical consumer-resource models, the producer density at equilibrium is constant and depends only on the consumer parameters. An increase in input I will thus only benefit the consumer density but not the producer density. Only the flux increases, *i.e.* the production, but not the standing stock. An increase of I accentuates the two associated destabilizing mechanisms of the paradox of enrichment: (i) the overproduction of the resource (here, the producer) due to the delay in the consumer regulation, followed by (ii) the over-consumption of the resource due to an increase of the consumer capacity to reduce the producer density to far below its equilibrium point (Murdoch *et al.* 2003). This can also be interpreted according to the principle of energy flux (Rip and McCann 2011): an increase of I will increase the relative energy flux supplying the consumer growth, and the biomass consumer-resource ratio, which is destabilizing.

The individual effect of each of the parameters on the ecosystem stability can be interpreted from the same perspective. An increase of the attack rate a_P or of the recycling rate r leads to the same result since it enhances the relative energy flux to the consumer; whereas an increase of b_P, e_N, e_P, e_D, or m_P stabilizes by slowing or reducing the intensity of this relative energy flux. The consumer parameters (a_C, b_C, e_C, m_C) can be either stabilizing or destabilizing because they act on both producer and consumer densities. Below a certain threshold, the increase of b_C, e_C, or m_C causes the increase of the primary production, and thereby the relative energy flux to the consumer, via producer density (see P equilibrium above). Beyond the threshold, the balance between direct negative effect on C (mortality and departure) and indirect positive effect (increase of its resource P thanks to lower regulation) shifts to the detriment of C density, so that over-consumption risk is reduced, relative energy flux decreased, and ecosystem stabilized. Note that a_C induces the inverse pattern with first stabilization at low values.

2.12 ONLINE APPENDIX B: SUPPLEMENTARY FIGURES

2.12.1 Multiple equilibria in heterogeneous metaecosystems

Spatial heterogeneity allows a continuum of stability for intermediate consumer diffusion rates (fig. B*1*, grey and orange areas). The same mechanism of stability than discussed in the text for Figure 4*A* is probably underlying this effect. The areas of multiple equilibria and of stability, is extended compared to the homogeneous case.

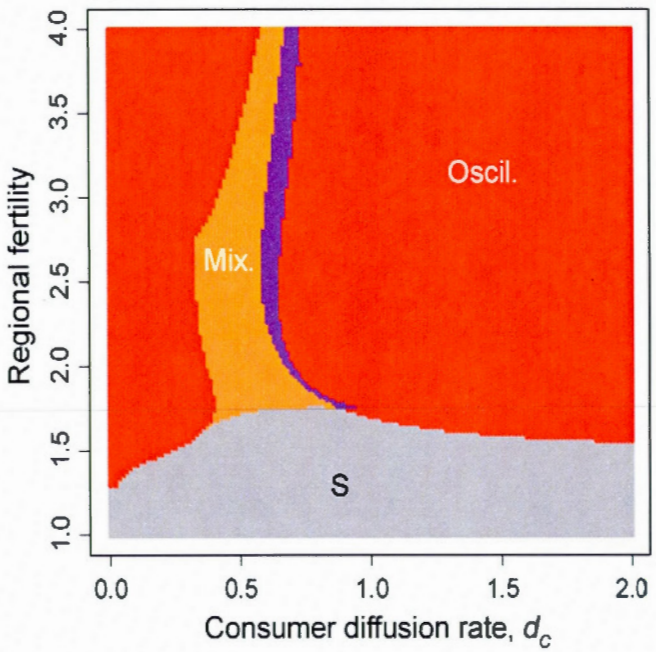

Fig. B1 Multiple equilibria in heterogeneous metaecosystems

Figure B*1* shows stability for an extended parameter space with regard to fig. 2*D* (consumer diffusion, d_C ranges from 0 to 2 and regional fertility ($(I_1 + I_2)/2$) from 1 to 4), for the heterogeneous case (ΔI=0.5). In the grey area (*S*), the equilibrium is stable ($\lambda max<0$). In the red area (*Oscil.*), the equilibrium is unstable ($\lambda max>0$). In the orange area (*Mix.*), there are both stable and unstable equilibria. In the purple area we found multiple equilibria, which are all unstable, some are symmetric, others asymmetric like for fig. 4*A*.

2.12.2 Spatial Synchrony

We analyzed how synchrony between ecosystem dynamics impacts the stability of the metaecosystem by computing an index to measure the time between two maxima of two dynamics (X_1 and X_2) relative to the period (which is the same for all dynamics):

$$PSI = 1 - min(|peaktime(X_1) - peaktime(X_2)|)\frac{4}{Period}$$

This phase synchrony index yields value of 1 for in-phase dynamics (synchronous), when the two maxima occur at the same time, and -1 for out of phase dynamics (hereafter called asynchronous) when the maximum of X_1 occurs at the same time as the minimum of

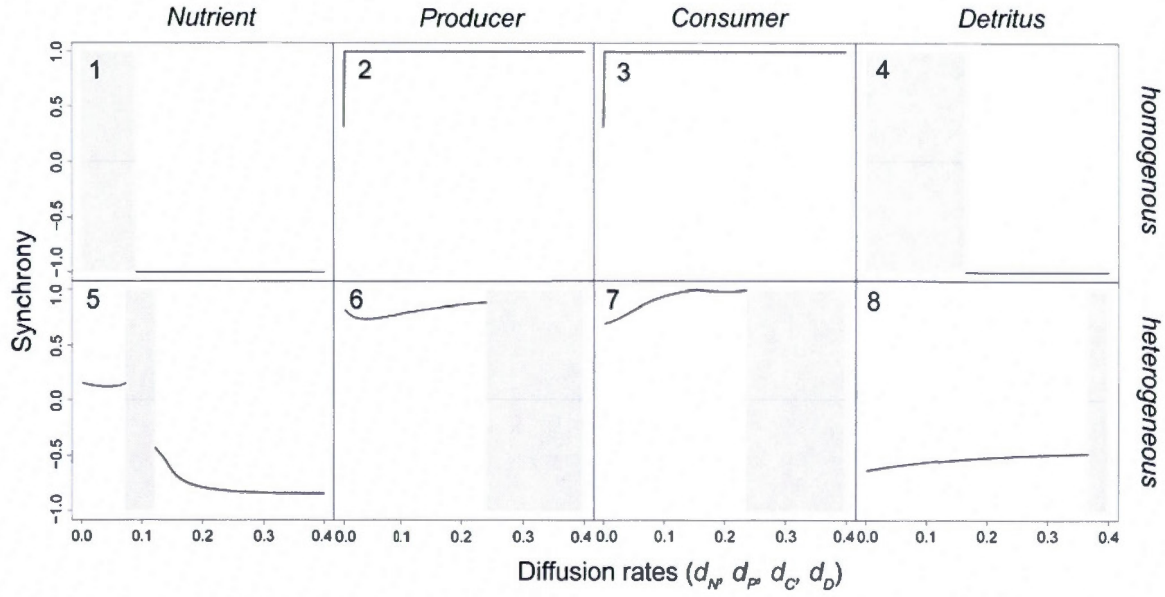

Fig. B2 Spatial synchrony with single spatial flows

Phase synchrony of consumer densities across ecosystems according to the diffusion rate of either nutrient, producer, consumer or detritus (columns from the left to the right), while the other diffusion rates are set to zero, for homogenous (top panels {*1,2,3,4*}) or heterogeneous (bottom panels {*5,6,7,8*}) metaecosystems (differences of fertility: ΔI=0 or ΔI=0.5, respectively). In the grey areas, the dynamics are stable and phase synchrony is no more relevant. Our phase synchrony index, *PSI*, yields value of 1 for dynamics oscillating in phase, -1 for dynamics oscillating in anti-phase. Regional fertilities: 1.35 for {*1,5*}, 1.47 for panels {*2,6*}, 1.50 for panels {*3,7*}, 1.39 for panel *4* and 1.23 for panel *8*. See Table 1 for other parameters.

X_2. Producer and consumer diffusion tends to sync up the dynamics, which reduces the effect of diffusion on stability, while nutrient and detritus diffusion lead to spatial anti-phase synchrony, which is destabilizing (fig. B2).

2.12.3 Detritus Inertia

The diffusion of detritus is destabilizing in homogenous metaecosystems and very slightly stabilizing in heterogeneous metaecosystems (fig. B*3*). Detritus do not directly participate to the destabilizing consumer-resource interaction. More detritus means a lower part of total nutrients involved in the destabilization process. Increase in the recycling rate decreases the density of detritus at equilibrium and is destabilizing, while increase in mortality rates of organisms and output rate of detritus increase the density of detritus at equilibrium and is stabilizing. Detritus spatial flows have a tenuous effect on stability. Changes in these three parameters displace the stability isoclines to higher or lower fertility threshold (with a more sensitive effect of mortality rates) but do not increase significantly the impact of detritus diffusion on stability.

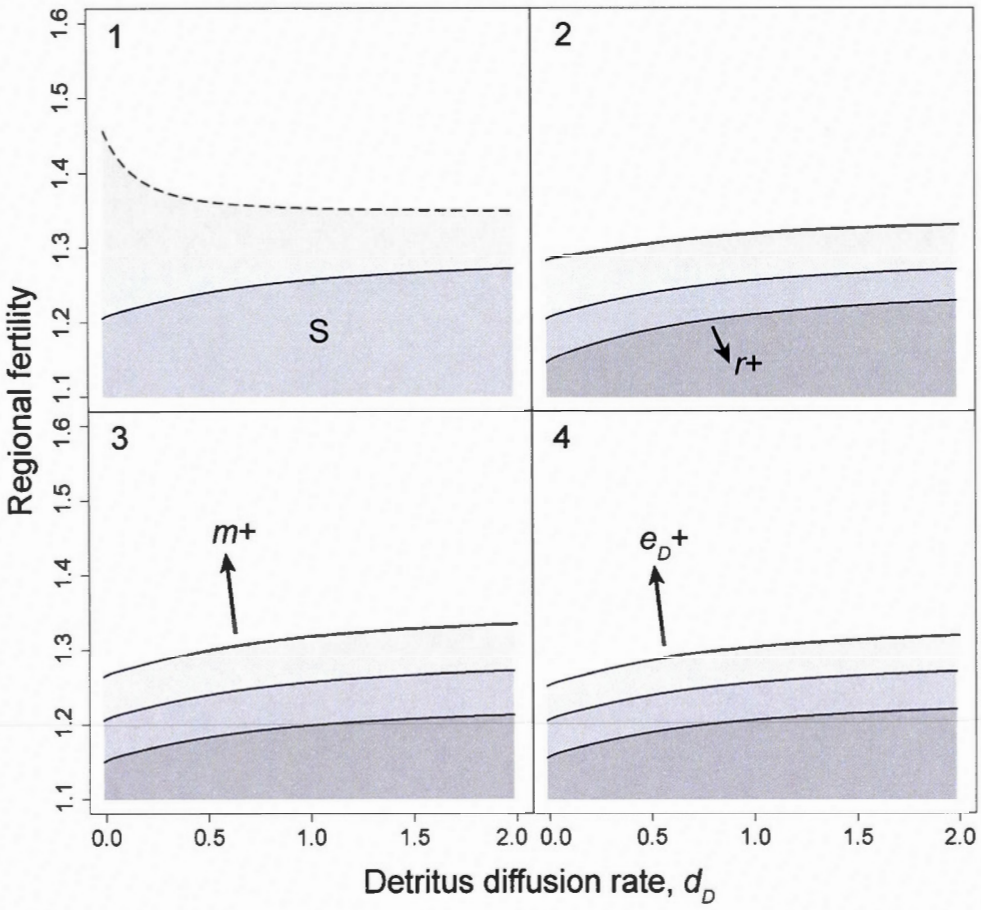

Fig. B3 Stability with spatial flows of detritus

Figure B*3* shows stability isoclines (λmax=0) for an extended parameter space with regard to fig. 2*B*: detritus diffusion, d_D, ranges from 0 to 2. In the grey area equilibria are stable (λmax<0). Panel *1*, shows the isoclines for the homogenous (dotted line, ΔI=0) and for the heterogeneous (solid line, ΔI=0.5) metaecosystems, with r = 0.5, m = m_P = m_C = 0.5, e_D = 0.1. Panel *2*, shows the isoclines when the recycling rate, r varies from 0.4 to 0.6. Panel *3*, shows the isoclines when the mortality rates, m = m_P = m_C, vary from 0.49 to 0.51. Panel *4* shows the isoclines when the output rate of the detritus, e_D varies from 0.08 to 0.12. For the panels *2*, *3* and *4*, the distribution of fertilities is heterogeneous (ΔI=0.5). See Table 1 for the other parameter values.

2.12.4 Stability and Non-linearity

The functional response of the producer saturates with the resource. This means that its per capita growth rate will increase less, for a same increase in nutrient availability, in high than in low fertility ranges. Consequently, it will be less efficient to exploit a high fertility. As a result, for the same regional fertility a heterogeneous metaecosystem will have a regionally lower regional primary productivity because of its rich ecosystem (fig. B*4*). Since the relative energy flux to the consumer will then decrease, this will be stabilizing, and inversely destabilization would require higher values of regional fertility.

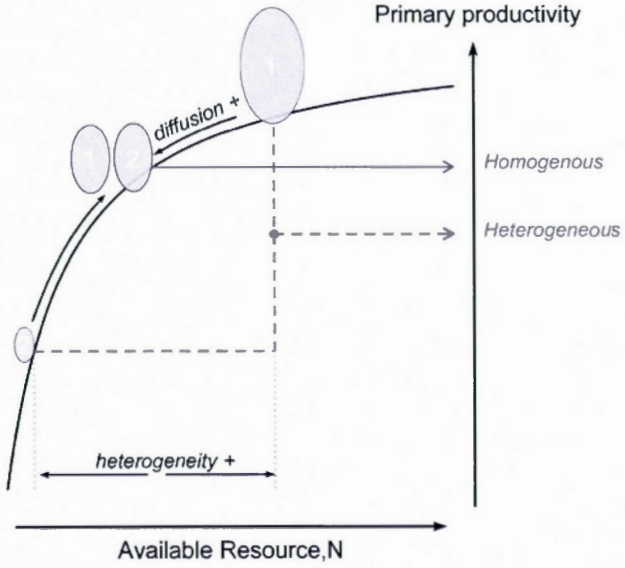

Fig. B4 Stability and Non-linearity

The producer has a non-linear functional response, making also non-linear the relationships between the local availability of the nutrient N (positively related with the input I in the isolated ecosystem), and the primary productivity in the ecosystem at equilibrium (solid line). The primary productivity is given by the functional response of the producer, f_P. The averaged primary productivity of the metaecosystem is represented in grey, for homogenous and heterogeneous distributions of inorganic resources. Homogenous metaecosystems, or heterogeneous ones whose inorganic resources have been homogenized by diffusion (curved black arrows), have a greater averaged primary productivity than heterogeneous metaecosystems, which is destabilizing according to the principle of energy flux (Rip and McCann 2011).

2.13 ONLINE APPENDIX C: SENSITIVITY ANALYSIS

We tested the robustness of our results to variability in other parameters than nutrient input (fertility) or diffusion rates. We performed two types of analyses:

- Spatial heterogeneity in demographic parameters;
- Variation of the functional responses of the producer and the consumer.

2.13.1 Spatial heterogeneity in demographic parameters

Our analysis focused on spatial heterogeneity in enrichment but species are also subject to spatial variation in their demographic parameters due to other environmental conditions. We explored how the stability isoclines are modified by adding heterogeneity in attack, saturation and mortality rates, of either the producer or the consumer. For each of these 6 scenarios we studied the stability of the metaecosystem with variation of regional fertility ($(I_1 + I_2)/2$) between 1.1 and 1.6 and the diffusion rates between 0 and 0.4. We considered both the cases of single spatial flows for each compartment (like in figure 2), and the case of equal diffusion rates for all compartments (like in figure 3). We also considered both homogenous and heterogeneous spatial distributions of fertility ($\Delta I \in \{0,0.5\}$). We implemented spatial heterogeneity in demographic parameters by fixing the parameter to 0.5 in one ecosystem and varying it between 0.4 and 0.6 in the other ecosystem. The interval was chosen such that coexistence was always possible and the stability isoclines visible in the $fertility \times diffusion$ window considered (excepted for some values with detritus diffusion).

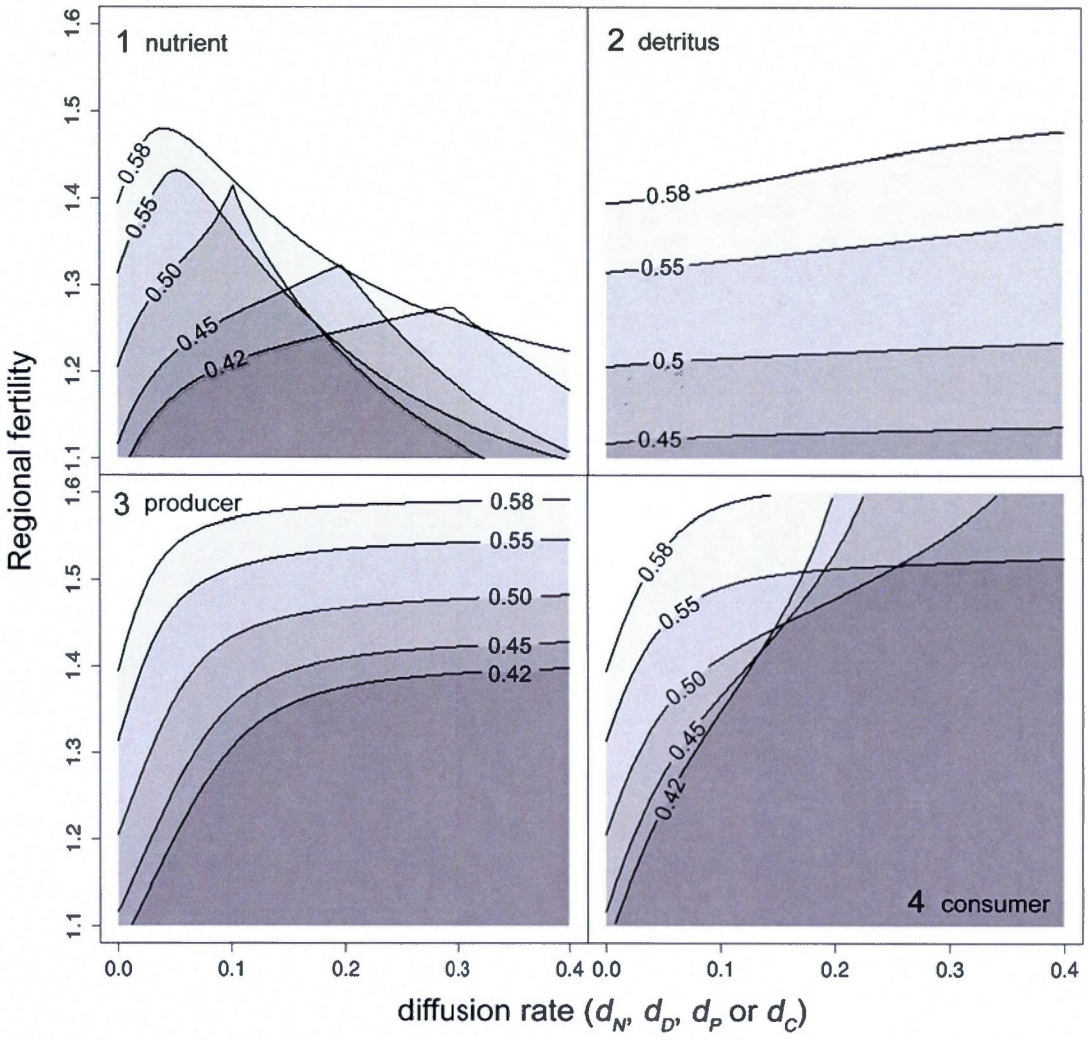

Fig. C1 Stability isoclines with spatial heterogeneity of producer mortality rate and single spatial flows

Each panel represents the stability isoclines (λmax=0) under changes of one diffusion rate (the others set to zero), either d_N, d_D, d_P, or d_C for panels *1*, *2*, *3* and *4* respectively, *versus* regional fertility of the metaecosystem ($(I_1 + I_2)/2$). In the grey area equilibria are stable (λmax<0). The distribution of fertility is heterogeneous, with $\Delta I = I_2 - I_1 = 0.5$. The mortality rate of the producer in ecosystem 1 is $m_{P_1} = 0.5$ and takes different values between 0.42 and 0.58 in the ecosystem 2 (noted on the isoclines). See Table 1 for symbols and other parameter values.

We found that the qualitative effects of diffusion of specific compartments on

stability are robust to the addition of heterogeneity in demographic parameters (see figure C*1* for a representative example with the heterogeneity of producer mortality rates).

The effect of spatial heterogeneity on demographic parameters depends whether it matches to the heterogeneity of fertility, that is to say, if both heterogeneities favor the productivity in the same ecosystem or not. If it is the case, the qualitative results are unchanged. For instance, the panel 1 of figure C*1* shows a representative example for heterogeneity in producer attack rates coupled or not with heterogeneity in fertility (solid and dotted lines), with the producer having a greater attack rate in the most fertile ecosystem. We found the same destabilizing effect of heterogeneity at low diffusion rate as in figure 3, and no stabilization at high diffusion rates. Similarly, these results for heterogeneity (and also its stabilization effect with single spatial flows, see figure 2) are robust to heterogeneity in demographic parameters if mortality or saturation rates of any of the two species is lower in the most fertile ecosystem, or if the attack rates are higher in the most fertile ecosystem. For the reverse scenario, the heterogeneity in demographic parameters might counteract sufficiently the heterogeneity of fertility to lead to qualitative changes in the outcome. The heterogeneous metaecosystem might be more stable than the homogenous one even with the homogenizing effect of multiple spatial flows (panel 2 of figure C*2*). This is explained by the fact that heterogeneity in demographic parameters is independent from diffusion. Thus the non-linear averaging mechanism, leading to the stabilization effect of heterogeneity, cannot be cancelled by diffusion homogenization, unlike with heterogeneity in fertility (see the discussion section "Non stabilizing heterogeneity" in the main text, and online appendix B*4*).

2.13.2 Variation in organisms functional responses

In our main analysis we have considered the same functional response for both the producer and the consumer. However, since the effects of heterogeneity rely on the saturation of the functional response of the producer, we tested robustness of our results to more realistic scenarios where the producer have a more or less saturating response compared to the one of the consumer. To implement this, we varied the saturation rate, b: the lower the rate, the less saturating the growth. We performed the same analysis than for figure 2, while exploring combinations of (b_P, b_C) with b_P ranging from 0.1 to 0.7 and b_C ranging from 0.3 to 0.6.

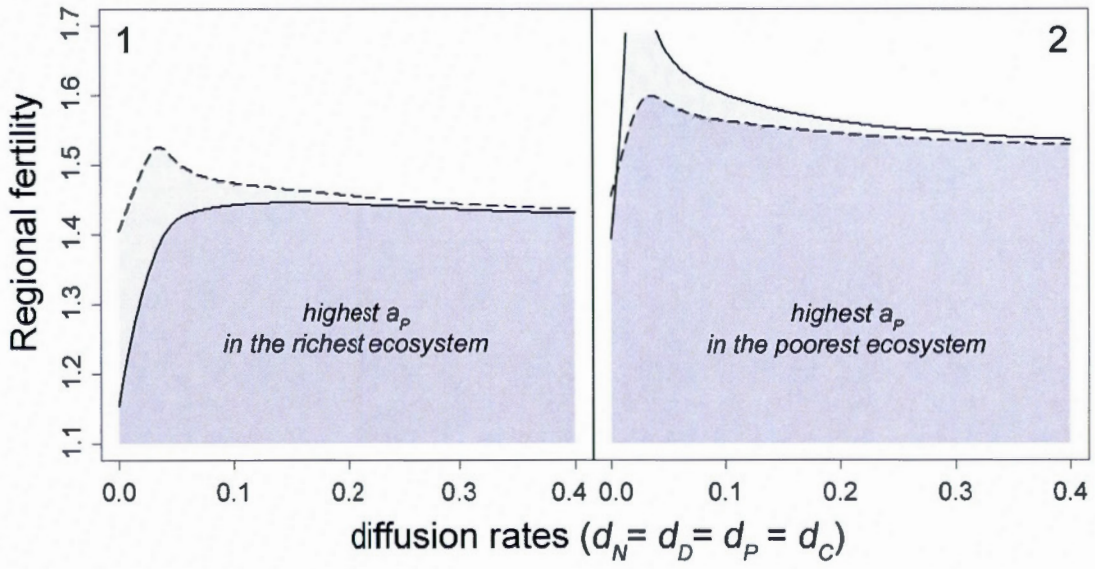

Fig. C2 Stability isoclines with spatial heterogeneity of producer attack rate and multiple spatial flows

Stability isoclines (λmax=0) under increasing diffusion for all compartments *versus* metaecosystem regional fertility ($(I_1 + I_2)/2$). Stability isoclines delimit the grey area where the equilibrium is stable for homogenous (dashed lines, ΔI=0) and heterogeneous (solid lines, ΔI=0.5) distributions of fertility. In panel 1, the attack rate of the producer is greater in the more fertile ecosystem: $a_{P_2} = 0.6$ and $a_{P_1} = 0.5$. In panel 2, the attack rate of the producer is lower in the more fertile ecosystem: $a_{P_2} = 0.42$ and $a_{P_1} = 0.5$. See Table 1 for other parameter values.

The results confirmed the crucial role of the non-linear averaging mechanism to

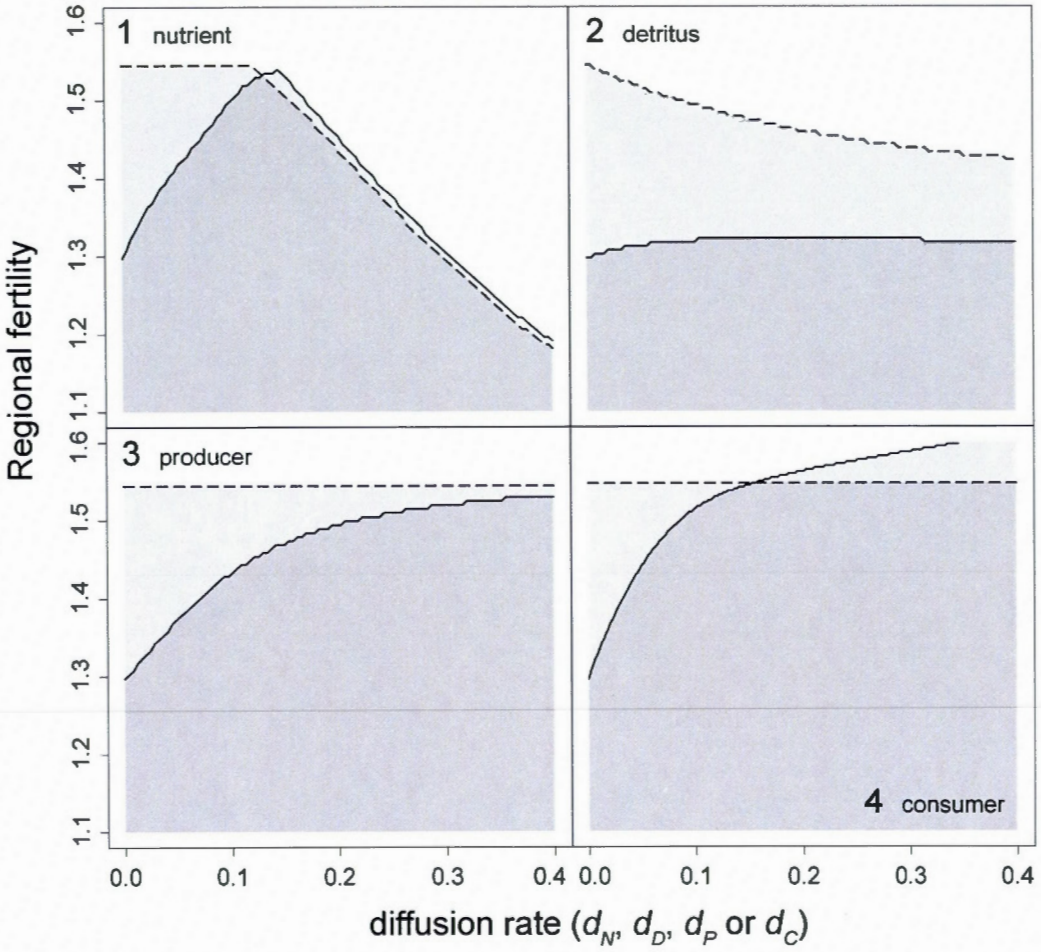

Fig. C3 Stability isoclines with single spatial flows and a less saturating functional response for the producer than for the consumer

Stability isoclines (λmax=0) under changes of one diffusion rate (the others set to zero), either d_N, d_D, d_P, or d_C for panels *1*, *2*, *3* and *4* respectively, *versus* regional fertility of the metaecosystem ($(I_1 + I_2)/2$). Stability isoclines delimit the grey area where the equilibrium is stable for homogenous (dashed lines, ΔI=0) and heterogeneous (solid lines, ΔI=0.5) distributions of fertility. Saturation rates are $b_P = 0.3$ for the producer and $b_C = 0.5$ for the consumer. Then the functional response is more saturating for the consumer than for the producer. See Table 1 for other parameter values.

stability. Figure C*3* shows the results when the producer has a less saturating response than the consumer. It shows that the stabilizing effect of heterogeneity (the area where the solid line is above the dotted one) is lower than in figure 2 where responses saturate at the same rate. At the opposite, the figure C*4* shows that the stabilizing effect of heterogeneity is increased (especially with nutrient or producer diffusion, panels 1 and 3), while the functional response of the producer is made more saturating compared to the one of the consumer. Hence, the more saturating is the functional response of the producer, the greater will be the effect of non-linear averaging. In addition, this effect will be accentuated if the functional response of the consumer is even less saturating, because it will be more effective in regulating the producer growth.

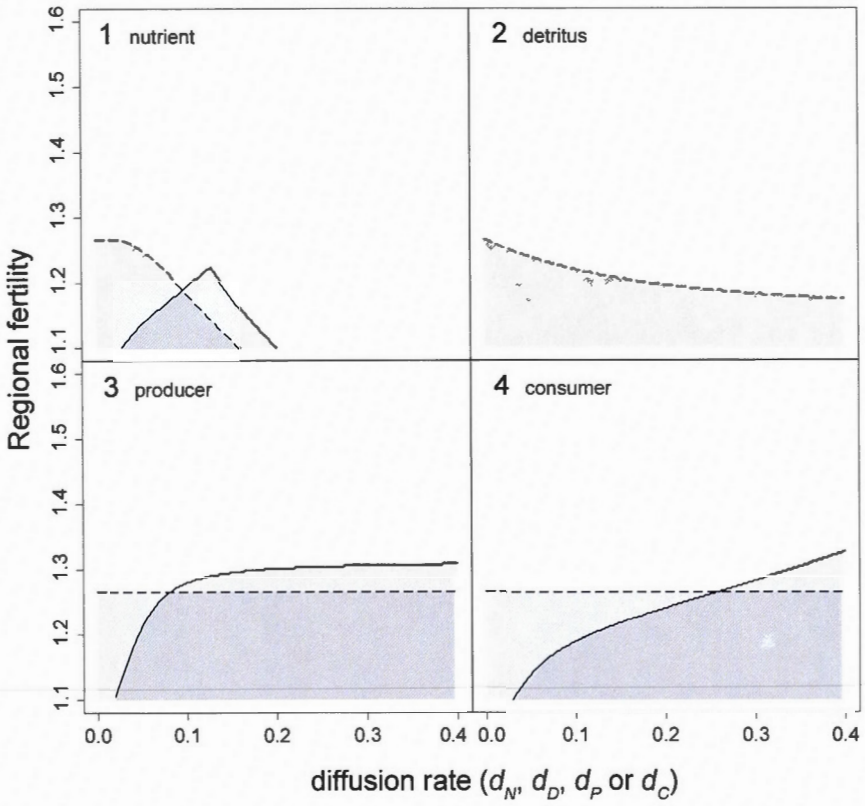

Fig. C4 Stability isoclines with single spatial flows and a more saturating functional response for the producer than for the consumer

Stability isoclines (λmax=0) under changes of one diffusion rate (the others set to zero), either d_N, d_D, d_P, or d_C for panels *1*, *2*, *3* and *4* respectively, *versus* regional fertility of the metaecosystem ($(I_1 + I_2)/2$). Stability isoclines delimit the grey area where the equilibrium is stable for homogenous (dashed lines, ΔI=0) and heterogeneous (solid lines, ΔI=0.5) distributions of fertility. Saturation rates are $b_P = 0.5$ for the producer and $b_C = 0.4$ for the consumer. Then the functional response is less saturating for the consumer than for the producer. See Table 1 for other parameter values.

2.14 ONLINE APPENDIX D: STABILIZATION WITH CONSUMER DIFFUSION

In heterogeneous metaecosystems, consumer diffusion has a specific stabilizing effect. We found that this stabilization is linked to combine effects acting in each of the ecosystems. In the richest ecosystem (the source) the emigration allows relaxing the consumer pressure. The production of consumers per unit of time and surface ($C_i f_C(P_i)$) finally decreases (fig. D*1*, panel 1). In the poorest ecosystem (the sink), the indirect density-dependence induced by the immigration shifts from positive to negative (fig. D*1*, panel 2). That is to say, the immigration brings more consumers when the local densities are low than when they are at their peak (fig. D*1*, panel 3). Note that the rate of diffusion is a constant, and then independent from local densities, but it can induce an indirect density-dependence on per capita growth rates. Indeed, the equation [3] giving the per capita growth rate is (with $i \in \{1,2\}$, referring to the ecosystems, see table 1 for other symbols):

$$\frac{1}{C_i}\frac{dC_i}{dt} = f_C(P_i) - (m_C + e_C) + \frac{d_C(C_{3-i} - C_i)}{C_i}$$

Therefore, the contribution of the spatial flows to the per capita growth rate depends on the local density (last term of equation [3]). To evaluate the indirect density-dependence this can induce, we plotted the contribution of spatial flows to the per capita growth rate

$$\frac{d_C(C_{3-i} - C_i)}{C_i}$$

against the local densities C_i normalized between 0 and 1 (fig. D*2*). If the slope of this curve is negative, hence the contribution of the spatial flows to the per capita growth rate is negatively related to local densities, inducing indirect negative density-dependence. Then we took the mean slope of this curve to evaluate the effect of diffusion on consumer density dependence. This proxy ranges from 1 for a positive density dependence, to -1 for a negative density dependence.

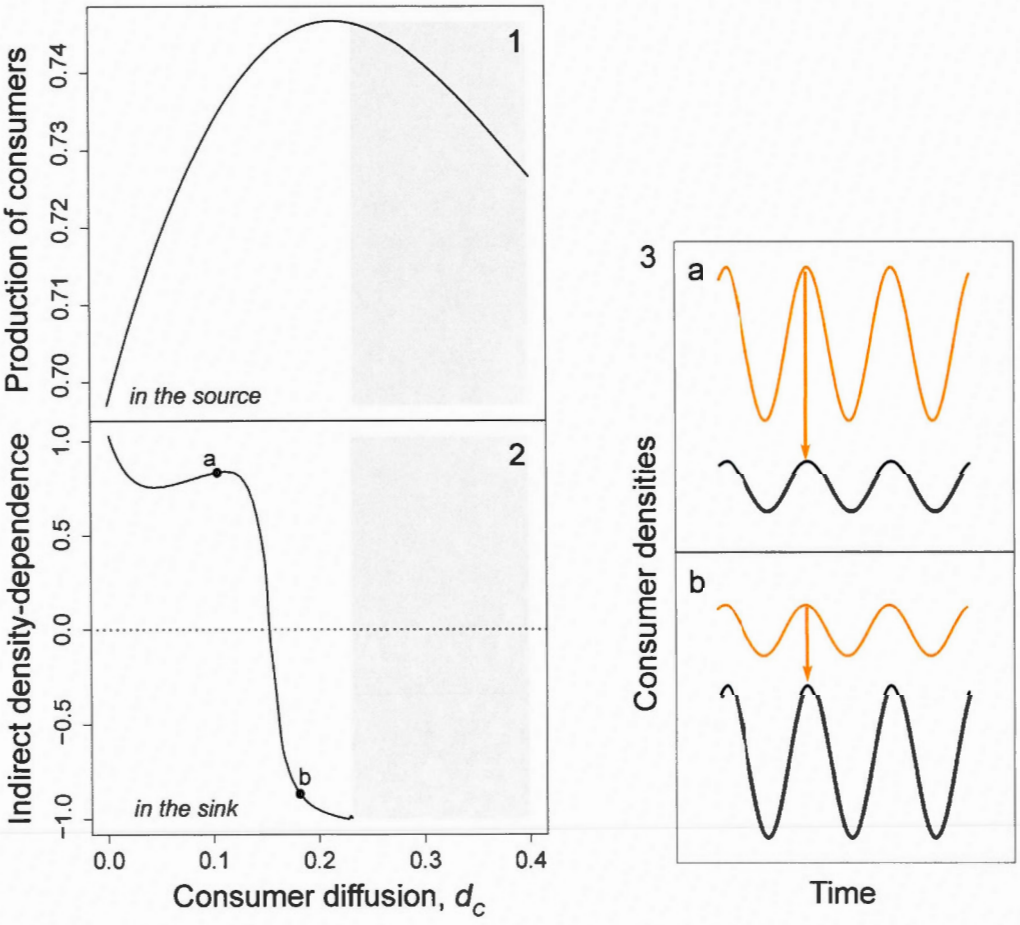

Fig. D1 Stabilization with consumer diffusion in heterogeneous metaecosystems
Panel *1* shows how the production of consumers per unit of time and surface ($C_i f_C(P_i)$) varies with consumer diffusion in the source ecosystem (with the higher fertility). The stabilization (grey area) matches with a decrease of consumer production. Panel *2* shows the indirect density dependence (IDD) induced by immigration in the sink ecosystem (the less fertile one). This IDD shifts from positive to negative with diffusion. Panel *3* illustrates this shift with hypothetical dynamics of the consumer in the source (orange lines) and in the sink (black lines) for a positive IDD (*a*) or a negative IDD (*b*). Arrows shows the spatial flow from the source to the sink at the density peak. In *a*, the arrows is at its maximum for the density peak, while in *b*, the arrows is at its minimum for the density peak. For panels *1* and *2* regional fertility is I=1.5, heterogeneity is ΔI=0.5 and see Table 1 for other parameter values.

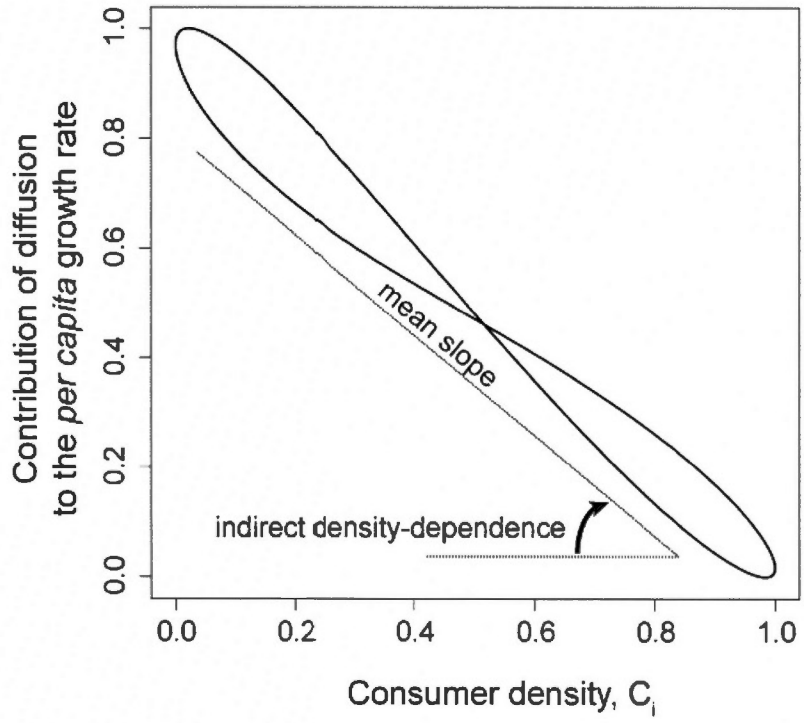

Fig. D2 Contribution of consumer diffusion to the density dependence of the consumer *per capita* growth

Figure D*2* shows the contribution of the diffusion to the consumer per capita growth rate $\frac{d_C(C_{3-i}-C_i)}{C_i}$ (with $i \in \{1,2\}$, referring to the ecosystems), against the consumer densities C_i. Densities are normalized between 0 and 1. We estimated the indirect density-dependence induced by consumer diffusion on the consumer per capita growth by the mean slope of this curve along a given period.

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CHAPITRE 3
ASSEMBLAGE DES ECOSYSTEMES (1) : MECANISME DE SELECTION ECOLOGIQUE

3.1 TITRE

Sélection des traits au cours de l'assemblage des réseaux trophiques – Le rôle des interactions et de la température

3.2 RÉSUMÉ

Comprendre les processus sous-tendant l'assemblage des communautés a été un thème central en écologie, bien qu'étudié de façon marginale pour les réseaux trophiques. Les modèles bioénergétiques ont été fondamentaux pour le développement de la théorie des réseaux trophiques. Ces modèles cherchent à reproduire des structures réalistes de réseaux trophiques, basés sur des relations allométriques, la température et des flux énergétiques explicites. Malgré leur popularité, on sait peu de choses sur les contraintes qu'ils imposent sur les dynamiques d'assemblages.

Dans cette étude nous analysons les conséquences du processus d'assemblage dans les réseaux trophiques sur la sélection des traits des espèces, en utilisant des variants d'un modèle bioénergétique, et en nous appuyant sur la théorie classique des dynamiques consommateur – ressource. Nous examinons la pression de sélection exercée sur la masse corporelle et l'efficacité de conversion des espèces, comment cette pression de sélection varie au cours de la séquence d'assemblage, et dans quelle mesure elle dépend de la température. Nous étudions d'abord analytiquement cinq différents modèles de chaînes trophiques, en déterminant comment les traits devraient être sélectionnés au cours de l'assemblage. Ensuite nous confrontons ces attendus à des simulations d'assemblages multi-espèces.

Nous trouvons que la sélection exercée par la compétition par exploitation et la compétition apparente est particulièrement sensible à la façon dont les flux trophiques sont représentés. De plus nous observons que l'on sélectionne systématiquement des masses corporelles plus petites à la base des réseaux trophiques, ce qui affecte la persistance des niveaux trophiques supérieurs. Les augmentations de température induisent d'importants changements dans la structure des réseaux, ce qui modifie la sélection des traits et renforce la compétition par exploitation. Nos résultats suggèrent qu'une plus grande attention devrait être portée aux effets de sélection écologique issus du processus d'assemblage pour mieux comprendre la diversité et le fonctionnement des réseaux trophiques réels, ainsi que leur réponse aux actuelles changements globaux.

Cet article intitulé « Trait selection during food web assembly – the roles of interactions and temperature » a été co-rédigé par moi-même, mes directeurs de thèse Dominique Gravel et Nicolas Mouquet, et la chercheuse Sonia Kéfi. Le manuscrit a été soumis pour publication en octobre 2014 dans la revue *Theoretical Ecology*.

En tant que premier auteure, j'ai réalisé la recherche bibliographique, l'étude analytique des modèles simples, la programmation des modèles de simulation, l'analyse des résultats ainsi que l'essentiel de la rédaction. Dominique Gravel, dernier auteur, et moi-même avons élaboré la problématique et le choix du modèle. Sonia Kéfi, second auteur a participé à la résolution des problèmes techniques sur le modèle, suggéré les méthodes d'analyse et participé à la rédaction. Nicolas Mouquet, 3ème auteur et Dominique Gravel ont également participé à la rédaction.

3.3 TITLE

Trait selection during food web assembly – The roles of interactions and temperature

3.4 ABSTRACT

Understanding the processes driving community assembly has been a central theme in ecology, yet marginally studied in food webs. Bioenergetic models have been instrumental in the development of food web theory. These models aim to reproduce realistic food web structure based on allometric relationships, temperature and explicit energy flows. Despite their popularity, little is known about the constraints they impose on assembly dynamics. In this study we build on classical consumer-resource theory, using variants of a bioenergetic model to analyze the consequences of food web assembly on the selection of traits. We investigate the selective pressure on body mass and conversion efficiency, how does this selection vary through the assembly sequence, and to what extent it depends on temperature. We first analyze five different simple food chain models, and identify how traits should be selected along assembly. Second, we investigate further these expectations with numerical simulations of multispecies assemblages. We find that the selection exerted by exploitative and apparent competitions is highly sensitive to how energy fluxes between consumers and resources are represented. Moreover, we consistently observe a selection of lower specific body masses at basal trophic levels, which is detrimental to the persistence of higher trophic levels. Increases in temperature induce important structural changes that modify trait selection and strengthen exploitative competition. Our results suggest that greater attention should be devoted to the effects of ecological selection on food web assembly to understand the diversity and the functioning of real food webs, as well as their possible response to ongoing global changes.

3.5 KEYWORDS

Food web, assembly, ecological selection, bioenergetic model, temperature

3.6 INTRODUCTION

Communities result from assembly processes during which species interact in various ways, exclude others, go extinct or coexist depending on their traits and their response to environmental conditions. Community assembly is a selection process that is likely to shape the distribution of species traits and ecosystem functioning (Fukami and Morin 2003, Fukami *et al.* 2010, Vanette and Fukami 2014). Surprisingly, despite the rich history of research on the assembly of competitive systems, such as plant communities (Götzenberger *et al.* 2012, Martin and Wilsey 2012), or on simple systems with few species, such as experimental communities of zooplankton or protists (Louette and De Meester 2007, Olito and Fukami 2009), very little is known about the assembly of large and diverse food webs (Bascompte and Stouffer 2009).

Consumer-resource theory has provided mechanistic tools to establish the conditions for species coexistence, or competitive exclusion, when a few species are interacting (Tilman 1982, Chase and Leibold 2003, Murdoch *et al.* 2003). Within a trophic level, coexistence is mainly constrained by exploitative and apparent competition, involving the relative efficiency of species to acquire resources and to withstand predation. Experiments and theory established that under exploitative competition, species with identical resources could not coexist indefinitely (so-called "competitive exclusion principle"; Gause 1934, Hardin 1960). The R* rule states that the species whose traits allow to reduce the equilibrium density of the resource (R*) to the lowest level will exclude all of its competitors (Tilman 1977, 1980, Tilman *et al.* 1981, Miller *et al.* 2005). In the situation of species sharing a predator, theory predicts that the species that can sustain the greatest density of predators will win the apparent competition (Holt *et al.* 1994, Holt and Lawton 1994, Holt *et al.* 2001, Chase *et al.* 2002, Chesson and Kuang 2008). Consumer-resource theory provided an extensive understanding of the dynamics of trophic interactions, and to a certain extent of the resource and predation constraints on biodiversity (Schmitz et al. 2000, Thébault and Loreau 2003, 2006, Shreiber and Rittenhouse 2004, Schmitz 2008). The consequences of exploitative and apparent competitions are clear in simple communities including a few species only (Chase and Leibold 2003, Murdoch *et al.* 2003).

However, there is currently no general understanding of coexistence mechanisms responsible for the assembly of food webs, in which complex indirect interactions operate simultaneously.

The disassembly of food webs has been greatly studied with the analysis of secondary extinctions in interaction networks (Solé and Montoya 2001, Dunne *et al.* 2002; Gross and Cardinale 2005, Montoya *et al.* 2006, Dunne and Williams 2009, Fowler 2010), but there is only a limited knowledge of food web assembly (Bascompte and Stouffer 2009). During the assembly of a food web, species interactions modify progressively the distribution of traits present in the food web. In particular, traits improving resource uptake should be selected as an outcome of exploitative competition, and traits of preys improving their resistance to predation should be selected as an outcome of predation pressure. We refer to this process as *"ecological selection"*. We do not consider specific evolution processes such as speciation or local adaptation, but only the selection of species traits due to ecological filtering after immigration from a regional pool. This process of ecological selection will eventually determine the food web composition. Despite this potential important role in shaping food webs, little theory has been developed on how ecological selection operates along the assembly process. Most of community assembly theory focused on the role of species arrival order in producing alternative stable communities (Luh and Pimm 1993, Law and Morton 1993, 1996, Lockwood *et al.* 1997, Fukami 2005), and on the role of diversity in driving resilience and resistance to invasion (Post and Pimm 1983, Case 1990, 1991, Law and Morton 1996, Morton and Law 1997, Capitán *et al.* 2011). Some experimental approaches have been developed (Jiang and Patel 2008, Olito and Fukami 2009, Fukami *et al.* 2010, Kadowaki *et al.* 2012) but without any theoretical formalization.

Here we investigate the selection of body mass and conversion efficiency over the course of food web assembly, and its sensitivity to temperature. Significant progresses have been made in the modeling of dynamical food webs thanks to the niche model (Williams and Martinez 2000) and to the metabolic theory of ecology (Brown *et al.* 2004). Yodzis and Innes (1992) have taken a step toward the mechanistic understanding of consumer-resource

dynamics, by setting the structure of bioenergetic models. An advantage of bioenergetics models is to parameterize them with easily measurable species characteristics (body size / body mass), and to limit the number of model parameters thanks to well-documented allometric relationships with many biological rates (Brown *et al.* 2004). Body mass and conversion efficiency are the key traits to describe the bioenergetic dynamics of trophic interactions. Body mass determines inflow (consumption) and outflow (mortality) rates, and conversion efficiency the proportion of inflow that a species is able to convert in new biomass. Moreover, the rate of these flows is known to strongly vary with temperature (e.g. Boyd *et al.* 2013). Vasseur and McCann (2005) extended bioenergetic models further by implementing the dependence of metabolism to temperature. This progress enables to investigate how changes in temperature affect species interactions and trophic flows in the food web (Vasseur and McCann 2005, Gilbert *et al.* 2014). Hence bioenergetic models have played a central role in the recent progresses of knowledge on food web dynamics and structure (Brose *et al.* 2006b, Petchey *et al.* 2008, Berlow *et al.* 2009, Brose *et al.* 2012). Previous studies have derived the equilibria of these models to study the stability of a consumer–resource interaction (Yodzis and Innes 1992, Vasseur and McCann 2005), but the analysis of their implications for coexistence in species-rich food webs has not been done so far.

In this study we integrate food web complexity and metabolic constraints to community assembly. Our objective is to understand trait selection over the course of food web assembly in the light of consumer-resource classical theory. We ask how do sequential assembly operate an ecological selection on the distribution of traits present in a food web. We apply R* and apparent competition theory to investigate trait selection in simple and tractable food web modules, at different temperatures. We then test our analytical predictions on simulated sequence of assembly multi-species food webs. We focus on systems of 2 to 3 trophic levels. We also investigate to what extent the selection of traits is sensitive to structural assumptions about the representation of energy flows in bioenergetic models. We more specifically address the mechanics of ecological selection through three questions: **Q1** – How are the key traits driving trophic interactions (e.g. body mass,

conversion efficiency) selected along community assembly according to basic ecological assumptions made on consumer-resource interactions? **Q2** – Do predictions drawn from simple food chain modules hold in more complex food webs? **Q3** – How would temperature affect the selection of species traits through species metabolism?

We find structuring effects of the assembly process on trait distribution, strongly influenced by indirect effects of temperature.

3.7 METHODS

3.7.1 Analytical study of simple food chains

We first perform invasion analyses on small food chain modules of 2 or 3 trophic levels to determine the traits allowing a primary producer to invade. From this, we then derive the expected direction of selection on each trait in the context of an assembly process made of successive invasion trials.

3.7.1.1 Model description

The basal trophic level is an inorganic resource, R (Fig. 1), supplied by an external constant input I (*e.g.* through weathering), and leached out at rate out_R. Trophic levels 2 and 3 are respectively a producer P and an herbivore H. Hereafter we refer to trophic structures with or without herbivores as RP and RPH structures respectively. The model describes the fluxes of nutrients among compartments and we assumed biomass to be directly proportional to nutrient content (equations detailed in Table 1). We do not consider omnivory for tractability.

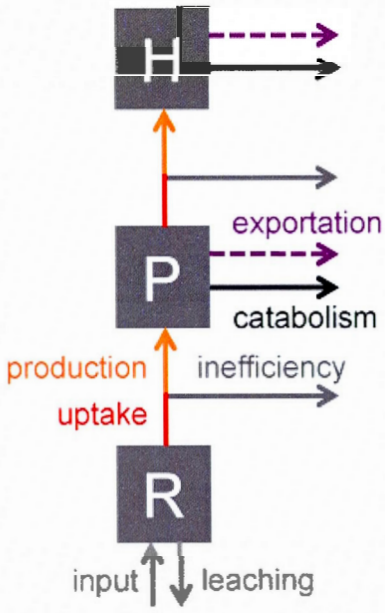

Fig. 1

In the analytical study, we consider food chain modules of 2, or 3 trophic levels: RP or RPH. R is an inorganic resource fed upon by a primary producer P. An herbivore H feeds on P. R is supplied by external inputs, and loses nutrients by leaching and uptake from P. Species convert a part of their uptake into new biomass (production) and the remaining is lost due to inefficiency during the uptake. Part of the new biomass is lost due to catabolism (mortality and detritus production), herbivory, or to other processes independent from metabolism (exportations: *e.g.* sedimentation, dispersal, *etc.*).

There are multiple ways to represent energy flows among the three trophic levels, and especially the efficiency of energy conversion into biomass. We therefore consider 5 variants of consumer-resource models (Table 1): a standard Lotka-Volterra equation (model 1) and four bioenergetic models with variations in the definition of nutrient fluxes between compartments (models 2-5). Model 1 is the simplest and has a structure common to all other models, without bioenergetics constraints. Species i uptake the resource at a rate a_i (uptake), a proportion ϕ_i of this uptake is converted into new biomass (production), and the

species loses biomass and dies at a rate m_i (catabolism). In the bioenergetic models 2-5, metabolism is explicitly modeled using allometric scaling with body mass and temperature. The maximum consumption rate (uptake, production) and the metabolic rate (catabolism) can both be written as a function of species body mass M_i and temperature T (Gillooly *et al.* 2001, Vasseur and McCann 2005): $a_z(T_0)M_i^{-0.25}e^{\frac{E(T-T_0)}{kTT_0}}$, with $a_z(T_0)$ the constant of the allometric relationship representing the physiological maxima measured at the reference temperature $T_0 = 20°C$ (see Table 2 for symbols).

Table 1

Model variants: Mathematical formulation of the different processes schematized at Fig. 1 (i.e. the different flows) for the 5 models considered, when a compartment *i is* fed upon by a compartment *j*, with B_i the density of compartment *i*. $Y_i = a_{y_{(T_0)}}M_i^{-0.25}e^{\frac{E(T-T_0)}{kTT_0}}$ is the maximum consumption rate and $X_i = a_{x_{(T_0)}}M_i^{-0.25}e^{\frac{E(T-T_0)}{kTT_0}}$ is the metabolic rate. Note that allometric constants $a_{x_{(T_0)}}$ and $a_{y_{(T_0)}}$ (for the biological rates measured at temperature T_0) are different between producers and herbivores but they do not vary within trophic level in multispecies simulations. Models 3 to 5 are variants of model 2 and the differences from model 2 are highlighted. The supply and losses of the inorganic resources are the same for all models: $I - out_R R_i$. Symbols are described in Table 2

	Model	Description	uptake	production	catabolism	exportation
	Model 1	Classical Consumer-Resource model	$-a_iB_iB_j$	$+a_i\phi_iB_iB_j$	$-m_iB_i$	-
Bioenergetics	Model 2	Efficiency in production	$-Y_iB_iB_j$	$+Y_iB_iB_j\phi_B$	$-X_iB_i$	-
	Model 3	Efficiency in uptake	$\frac{-Y_iB_iB_j}{\phi_i}$	$+Y_iB_iB_j$	$-X_iB_i$	-
	Model 4	Edibility of the resource	$-Y_iB_iB_j$	$+Y_iB_iB_j\psi_A$	$-X_iB_i$	-
	Model 5	Supplementary losses	$-Y_iB_iB_j$	$+Y_iB_iB_j$	$-X_iB_i$	$-out_iB_i$

Table 2
Symbols and values of the parameters used for the simulations. In the "Values" column, U refers to a uniform distribution

Symbols	Description	Dimensions	Values
R, P, H	Densities[1] of the compartments: Inorganic Resource, Producer, Herbivore	$M.L^{-2}$	-
I	Input of inorganic nutrient	$M.L^{-2}.T^{-1}$	1
out_i	Output rate of species or resource i	T^{-1}	0.1
M_i	Specific body mass of species i	M	$\mathcal{U}[10^{-8}, 10^{8}]$
T	Temperature	Θ	$\{0,20,40°C\}$ used in °Kelvin
T_0	Reference temperature	Θ	$20°C$
E	Activation Energy	$M.L^2.T^{-2}$	$0.62eV$ (Gillooly *et al.* 2001)
k	Constant of Boltzmann	$M.L^2.T^{-2}.\Theta^{-1}$	$8.61 \times 10^{-5} eV.K^{-1}$
ϕ_i	Conversion efficiency of species i.	*dimensionless*	$\mathcal{U}[0,1]$
ψ_i	Edibility as a resource of species or resource i in model 4.	*dimensionless*	$\mathcal{U}[0,1]$
$a_{x_{i(T_0)}}$	Allometric constant for the metabolic rate of compartment i measured at temperature T_0. The same constant is used for all species of the same trophic level (P or H)	$T^{-1}.M^{1/4}$	P: 0.138 H: 0.314 (Brose *et al.* 2006b)
$a_{y_{(T_0)}}$	Allometric constant for the maximum consumption rate of compartment i measured at temperature T_0. The same constant is used for all species of the same trophic level (P or H)	$T^{-1}.M^{1/4}.(M.L^{-2})^{-1}$	P: 1 H: 2.512 (Brose *et al.* 2006b)
a_i	Uptake rate of species i in model 1.	$T^{-1}.(M.L^{-2})^{-1}$	$\mathcal{U}[0,1]$
m_i	Mortality rate of species i in model 1.	T^{-1}	$\mathcal{U}[0.01,1]$

[1] *Note that density means stock or biomass by unit of surface, not abundance of individuals*

For the sake of simplicity we assume identical allometric constants for the different species of a given trophic level, and identical activation energy E for biological rates of all

species, even though we are aware of recent experiments documenting differences among trophic levels (Rall *et al.* 2012). The activation energy is set to 0.62eV, a mean value across many organisms groups (Gilooly *et al.* 2001, Vasseur and McCann 2005). The bioenergetic model 2, is a simple transposition of the classical consumer-resource model 1 with allometric scaling. In model 3 we change the way species conversion efficiency, ϕ_i is accounted for: In models 1 and 2 we multiply the production by ϕ_i, stating that the species produces ϕ_i units of biomass per unit of resource. A less intuitive approach, but also the most commonly used in recent bioenergetic models, is to divide the uptake by ϕ_i (model 3), stating that the production of 1 unit of consumer requires $1/\phi_i$ units of the resource. This distinction appears trivial because the ratio of units of consumer produced to resource uptake is the same, but since the equilibrium densities differ between models 2 and 3, this assumption may impact the exploitative competition expected during an assembly process. The ratio of production by unit of uptake can also be perceived as a function of resource edibility ψ_i rather than consumer conversion efficiency. The more edible is the resource, the greater will be the production of consumer biomass (model 4). In this case, the conversion efficiency is a property of the prey, not the predator. Finally, we add a last model, #5, where nutrients can also be lost at a rate out_i independent from species catabolism. This encompasses many common processes such as for instance sedimentation in aquatic systems or predation by species not explicitly considered here.

3.7.1.2 Trait selection

We perform invasion analyses to understand how body mass and uptake efficiency should be selected during an assembly process (Appendix A). For each trophic structure (RP and RPH, *i.e.* without or with herbivores) and at each trophic level (R, P and H), we consider the situation where an invader tries to settle in the food chain when the system is at equilibrium (all equilibria are presented in Table 6 in Appendix B). We assume that the invader shares the same resource and the same predator as the resident species. We determine the traits promoting invasion, and hence the exclusion of its competitor (Table 3, and Appendix A). For the simplest case of the upper trophic level, the outcome of

exploitative competition is equivalent to the R* rule (Tilman 1982), and the traits are selected such that they minimize the density of the species resource at equilibrium, excluding the competitor by starvation. For the invasion of a producer when the herbivore is present, apparent competition also contributes to the net interaction and thus coexistence (Holt *et al.* 1994, 2001, Chesson and Kuang 2008). We derive the condition of invasion from the equations of the colonizer while the community is at equilibrium (see Table 6 in Appendix B). In the case of bioenergetic models, we also analyze how an increase in temperature would affect the equilibrium densities by boosting the biological rates, because such variations may impair the availability of food for the consumer species, and its resulting persistence.

3.7.2 Simulations of multispecies assemblages

The sequential arrival of new species may induce a succession of competition events where some species are excluded because of less favorable traits. We test whether the assembly of simulated food webs actually fit the selection of traits observed in our analysis of simple modules.

Trophic interactions are determined using the niche model (Williams and Martinez 2000). A niche position is assigned to each species, and species consume all the other species which position falls into their diet range. For model 1, the niche position varies between 0 and 1 and herbivores consume producers according to the rules described in Williams and Martinez (2000). For the bioenergetic models 2-5, the niche axis is the log10 of species body mass. The niche optimum of an herbivore of a given body mass is given by the linear empirical relationship between prey and predator body masses (Brose *et al.* 2006a). The boundaries of its range are given by the 10% and 90% quantile regressions (Gravel *et al.* 2013). The niche optimum of primary producers is randomly chosen between 1 and 10 (the numbers assigned to the inorganic resources). The width of their range is chosen such that they could eat 1 to 3 resources. When a species feeds on more than one resource, we divide the uptake uniformly across the resources with a preference parameter $\omega = 1/\#resources$ to avoid giving a competitive advantage to generalist species. We

draw species traits from uniform distributions, between 0 and 1 for conversion efficiency, edibility (model 4) or attack and mortality rates (model 1), and between -8 and 8 for the log10 of body mass (models 2-5). Other parameters are kept constant (see Table 2 for values).

We initialize our simulations with an empty ecosystem having ten inorganic resources, representing different niches for primary producers. We then add species one by one with a low initial density (10^{-4}). During one assembly step, successive invasion trials are performed until one is successful. For each of these invasion trials we compute the new interaction matrix integrating the invader. We describe the variation through time of the densities of each compartment of the resulting ecosystem (inorganic nutrients and species) by a system of ordinary differential equations whose form depends on the model according to Table 1. We then run the numerical integration with the algorithm Runge-Kutta Kash Carp of the gsl 1.15 library (Galassi *et al.* 2011) until we reach equilibrium. We detect equilibria by comparing averages on two successive windows of 500 integration steps (some simulations have non-linear dynamics). Equilibrium is reached when the absolute difference for each compartment between successive time windows is less than 10^{-11}. We consider species extinct when density falls below a threshold of 10^{-6} units of biomass (far below the expected equilibria).

We first run 50 simulations of competitive communities (with only primary producers) for each model, to check that the trait selection occurred as predicted analytically, but for the multispecies RP structure. We stop the assembly either when, after 10 initial assembly steps, a trait under selection varies less than 5% of the averaged value over all resident species, or after 10000 unsuccessful invasion trials within a step. We add the rule that an invader has to double at least its initial density to be successful in models 3 and 4. We find for these models (see analytical results) that the competition among producers is neutral and thus does not depend on traits. After few assembly steps, during which species share the amount of available resources according to their biological traits, the invading species simply stays at its initial density after having slightly disturbed the system. This would lead, at the end, to an artificial community with all densities near the

extinction threshold. We plot the variation of species traits along assembly to observe their potential deviation from the uniform distribution. We then focus on model 2 (bioenergetic model with conversion efficiency in consumer equation) to examine the effect of temperature (T) and trophic structure. We assemble 200 communities composed of producers and herbivores (RPH) for each of 3 contrasted temperatures (0, 20 and 40°C). We stop the assembly at the step 200 and we analyze how the distribution of the traits of all species in the final communities deviates from the analytical expectation.

3.8 RESULTS

3.8.1 Trait selection and structural sensitivity

We find that the traits selected at the upper trophic level of the food chain vary significantly between models (Table 3; plant trait column for RP structure and Herbivore trait column for RPH structure). Since there is no predation on the upper trophic level, the selection at this level is driven only by exploitative competition. The outcome of the competition relies on the equilibrium of the resource (R* or P* for RP or RPH models respectively), which is equal to the ratio of nutrient output to nutrient input rates flowing through the consumer species. For model 1, the resource equilibrium is a function of all the parameters of the consuming species (namely, attack, mortality rates and conversion efficiency), and hence the selection pressure acts on all of them. By contrast, in the bioenergetic models, the resource equilibrium can be independent from the consumer body mass if it contributes in the same way to inputs and outputs (models 2 and 3). Body mass is under selection only when there are outputs independent from the consumer metabolism (Table 3 model 5, Fig. 2n). In that case, the selection favors the species with the lowest mass-independent nutrient loss compared to the catabolic loss. Exploitative competition also promotes the selection of more efficient species in model 2. Conversely no selection on body mass operates when consumer biomass production does not depend on consumer conversion efficiency (models 3 and 4). Finally, producers with smaller body masses have greater chances of outcompeting the resident producer, independently of the model, with

the addition of herbivores (Table 3, plant trait column, RPH structure, models 2-5). Thus, under herbivory trait selection becomes less sensitive to models for basal species.

Table 3
Direction of the trait selection, as derived from the invasion analysis (Appendix A) on small food chains (Fig. 1), for each of the five models (1 to 5) and for both RP and RPH structures. An upward arrow indicates selection of greater values of the trait, while downward arrows means indicates selection of lower values. Note that equilibria are not tractable for model 5, RPH structure and therefore not presented.

Structure	Models	Plant traits	Herbivore traits
RP	Model 1	$m_P \downarrow, a_P \uparrow$ et $\phi_P \uparrow$	
	Model 2	$\phi_P \uparrow$	
	Model 3	$\emptyset$	
	Model 4	$\emptyset$	
	Model 5	$M_P \downarrow \phi_P \uparrow$	
RPH	Model 1	$m_P \downarrow, a_P \uparrow$ et $\phi_P \uparrow$	$m_H \downarrow, a_H \uparrow$ et $\phi_H \uparrow$
	Model 2	$M_P \downarrow \phi_P \uparrow$	$\phi_H \uparrow$
	Model 3	$M_P \downarrow$	$\emptyset$
	Model 4	$M_P \downarrow$	$\emptyset$

3.8.2 Trophic complexity relaxes the strength of selection

Multispecies simulations of competitive communities support our analytical predictions (Fig. 2). Traits under selection reach their minimum or maximum in the direction predicted by the invasion analyses within about fifty colonization steps, while the other traits remain close to the expectation of their distribution. We note that the selection pressure is relaxed when two traits are selected in the same direction (e.g. attack rate and

efficiency in model 1; Fig. 2c). Finally, producer diversity quickly saturates around the number of inorganic nutrients (Fig. 2 panels a, d, m). When no selection operates on the traits, the first arrived preempt the resources. A later arriver may succeed in settling by slightly deviating the system from its equilibrium but would not be able to grow or to stand disturbances. Then, if we only account for invaders that can grow, assemblies stop quickly (Fig. 2, models 3 and 4).

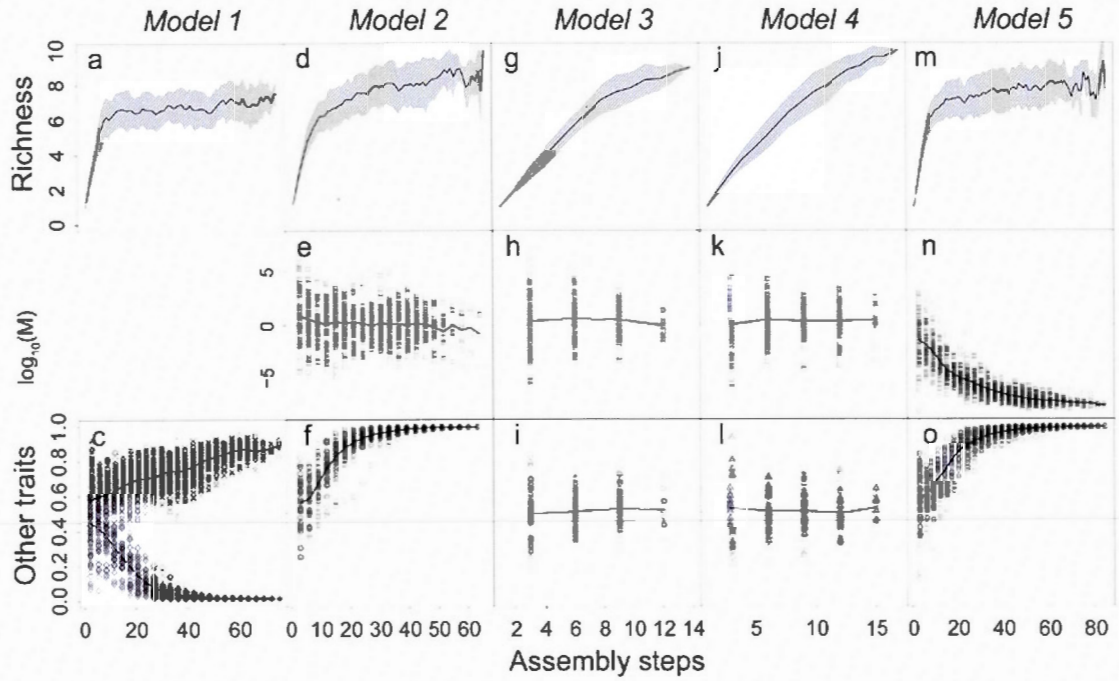

Fig. 2

Variation of species richness (top panels), $\log_{10}$ of specific body mass (intermediate panels, squares), and different other traits (bottom panels), along primary producers assembly (RP trophic structure), for each of the 5 model considered, in columns. Table 1 details the models. Solid lines indicate the averaged values over 50 simulated assemblies. Grey areas indicate standard deviation around the average (top panels). Grey points indicate the trait averaged value over all the species of a community at a given assembly step (one simulation): panel c, crosses for attack rate and diamonds for mortality rate; panels c, f, i and o: circles for conversion efficiency; panel l, solid triangles for edibility. The horizontal dotted line gives the expectation for the mean from the uniform distributions used to generate species traits.

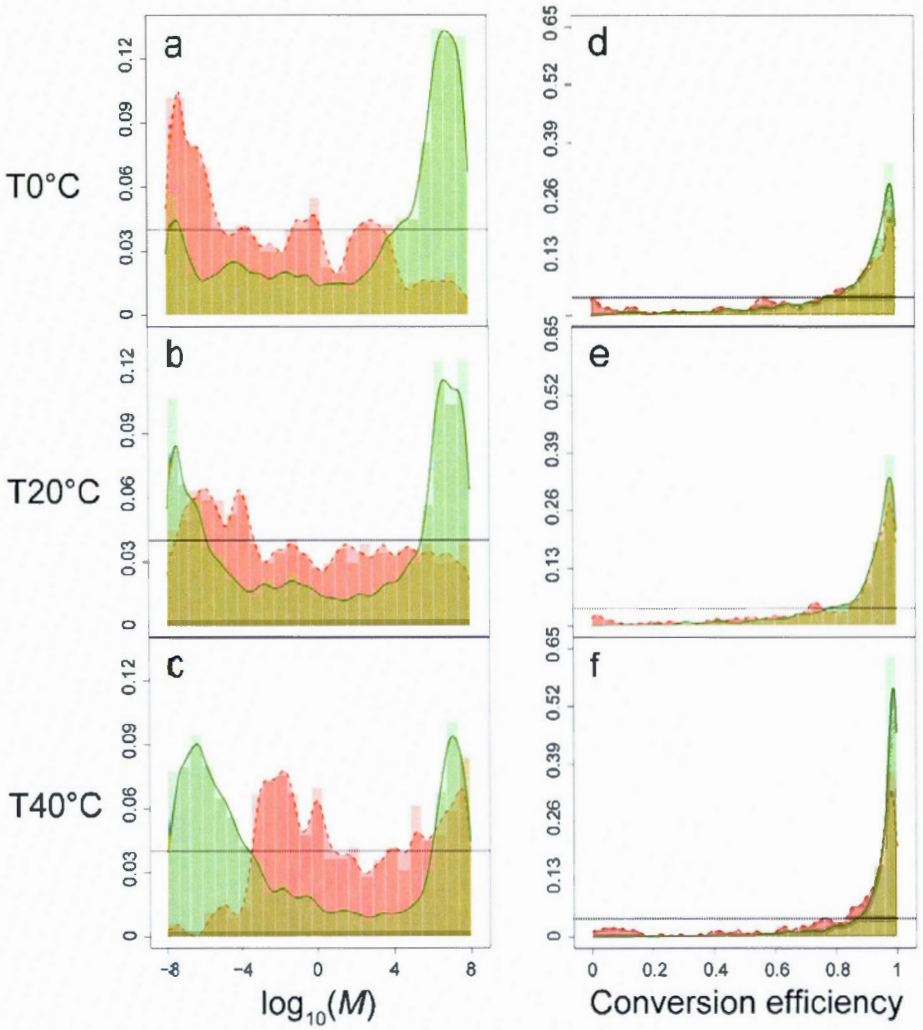

Fig. 3

Frequency distributions of the logarithm of body mass (left panels) and conversion efficiency (right panels) of primary producer (solid green lines) and herbivore species (dashed red lines) of 200 assembled 3-trophic-level food webs (RPH structure) at the end of the assembly (step 200), for temperature of 0, 20 and 40°C, with model 2 (bioenergetic model with efficiency at the production). The horizontal dotted line gives the uniform distributions used to generate species traits.

Our analytical study of modules predicts that small producers are promoted when adding herbivores. Instead, numerical simulations of model 2 show a bimodal distribution of the producer body masses at the end of the assembly process (Fig. 3b green solid line). A

cluster of large invulnerable producers is always present. When we look only at producers consumed by herbivores (Fig. 4b, dark dotted line), the distribution is clearly biased to smaller body masses, which is congruent with the analytical predictions. The bimodal distribution of producer body mass, observed at Fig. 3 (left column), results from a mixture of primary producers experiencing herbivory, which have relatively small body masses (Fig. 4 dotted lines), and primary producers free of herbivory (Fig. 4, solid lines), which have either very large or very small body mass. The simulations also show that when herbivores are present, the strength of the selection on conversion efficiency is relaxed: we observe a larger variance in RPH structure (Fig. 3e) than in RP structure (Fig. 2f at step 60). This variance of efficiencies, as well as the distribution of body mass, depends crucially on temperature (next section).

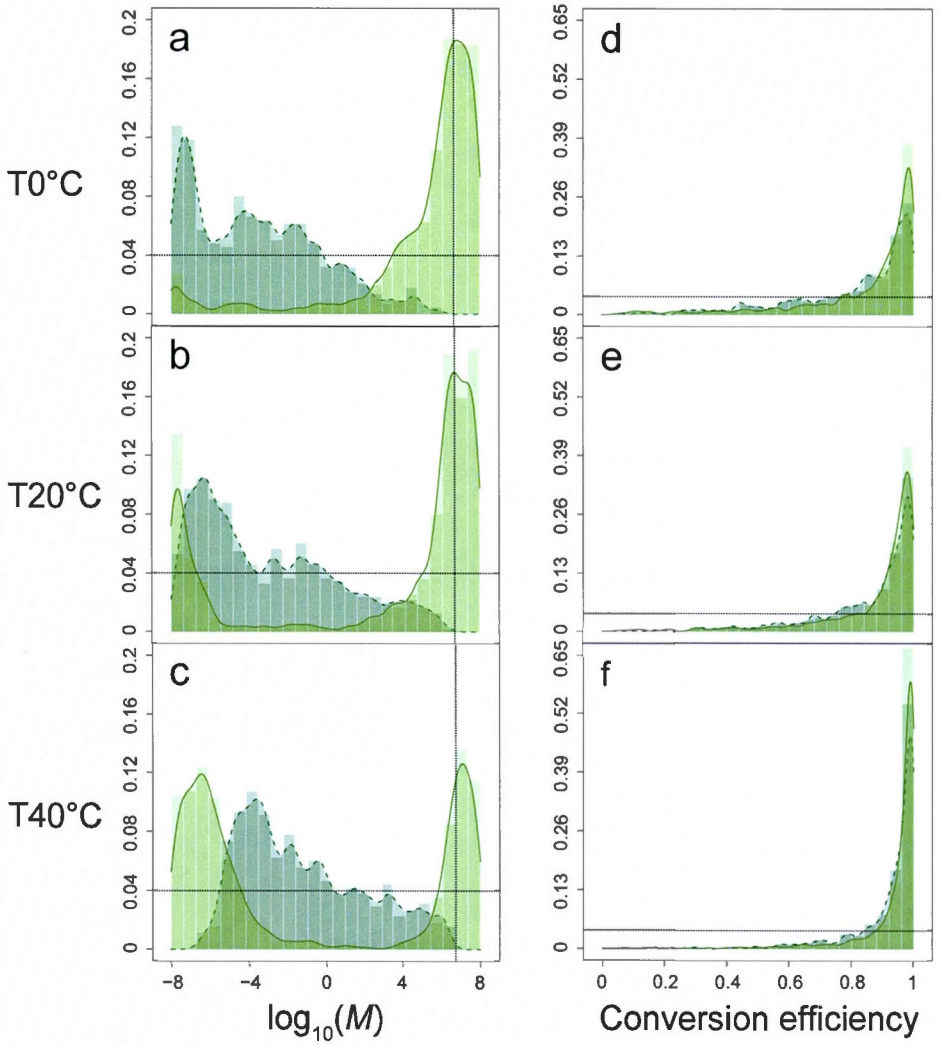

Fig. 4

Frequency distributions of the logarithm of body mass (left panels) and conversion efficiency (right panels) of producers free of herbivory (solid light green lines) and under herbivory (dashed dark green line) of 200 assembled 3-trophic-level food webs (RPH structure) at the end of the assembly (step 200), for temperature of 0, 20 and 40°C, with model 2 (bioenergetic model with efficiency at the production). The food webs are the same as in Fig. 3. The horizontal dotted line gives the uniform distributions used to generate species traits. The vertical dotted lines at the right of left panels are the critical producer body mass above which none of the herbivores over all 200 simulations can feed on.

Table 4
Changes in equilibrium densities with increased temperature. Again, equilibria are not tractable for model 5 with RPH structure and thus not presented.

Structure	Models	R^*	P^*	H^*		
RP	Model 2	∅	$P^* \downarrow$			
	Model 3	∅	$P^* \downarrow$			
	Model 4	∅	$P^* \downarrow$			
	Model 5			$R^* \downarrow$	non-linear[1]	
RPH	Model 2			$R^* \downarrow$	∅	$H^* \downarrow$
	Model 3			$R^* \downarrow$	∅	$H^* \downarrow$
	Model 4			$R^* \downarrow$	∅	$H^* \downarrow$

[1]see Appendix C

3.8.3 Indirect effects of temperature on trait selection

We investigate the effect of temperature on the strength of selection. An increase in temperature induces a decrease in some equilibrium densities (Table 4, see Fig. 7 in appendix C), which may have strong indirect effects on trait selection. Actually, multispecies assemblages using model 2 show striking indirect consequences of an increase in temperature (Figs. 3 and 4). The proportion of small primary producers raises with temperature, while the smallest herbivores can not maintain themselves and disappear (e.g. compare panels a, b and c in Fig. 3). Increased temperature also promotes the emergence of invulnerable small primary producers. The reduction of their equilibrium biomass leads the herbivores of smallest body mass to extinction by starvation (Appendix D). Moreover, conversion efficiencies of both producers and herbivores are more strongly selected at high temperatures, as shown by the reduced variance in conversion efficiencies (Figs. 3 and 4,

panels f). Overall, at warmer temperatures the interactions between residents and invaders during the assembly process selects smaller producers and larger herbivores, with highest conversion efficiencies for both.

3.9 DISCUSSION

Our results show that food web assembly promotes the selection of small species with high conversion efficiency. However, which trait is under ecological selection strongly depends on the structure of the model. Moreover, in bioenergetic models, the trophic structure and indirect effects of temperature constrain body mass and conversion efficiency distributions. We discuss below these points and their congruence with empirical observations. We finally propose future research directions to deepen the study of ecological selection with food web assembly models, and explicit its consequences for ecosystem functioning.

3.9.1 Sensitivity of trait selection to the model structure

One first striking result we find is the sensitivity of trait selection to assumptions about the representation of energetic flows. What appears trivial at first glance, the comparison between different formulations of conversion efficiency (models 2 *versus* 3) reveals a strong impact on the equilibrium densities. The resource equilibrium, the R*, also quantifies the competitive ability of a species for this resource (Tilman 1977). The conversion efficiency of the species enters the R* when multiplied with the consumption (model 2), but not when dividing the uptake (model 3). Subsequently, in the latter case successive competition events select more efficient species, whereas in the former invasion success does not depend on species traits. Species arriving later are not able to increase in abundance due to resource preemption. They may be able to persist in the system at low density but would not stand stochastic disturbances and some would inevitably be subjected to drift (Gravel *et al.* 2011). As a consequence, the selection becomes neutral and food web trait distribution results from the order of species arrival. In addition, we find that mass-

independent loss of biomass determines if smaller species body masses are selected or not (models 2 versus 5, Fig. 2). Since body mass sets who eats whom in bioenergetic models, the selection of smaller body masses when including mass-independent losses should heavily impact network structure by reducing food availability for higher trophic levels. This suggests that food web studies performed with bioenergetic models should discuss their results in the light of selection effects induced by their basic ecological assumptions.

However, our results also suggest that trophic complexity tempers this sensitivity of trait selection to structural assumptions: smaller body masses of producers are selected in all models (2-5). Therefore, the structural sensitivity we find would hold only for competitive communities (RP) or for upper trophic levels in diverse networks. Moreover, our simulations show that the strength of selection is relaxed for herbivores compared to producers. Other factors such as energy dissipation across trophic levels, and sensitivity to cascade extinctions may alter the impact of exploitative competition at the upper trophic level, by increasing species turnover.

3.9.2 Constraints by predation on prey body mass

Smaller body masses of producers are selected in all bioenergetic models when herbivores are present. In tri-trophic food chains, the best competitors at the intermediate level (here the producer) must be able to stand high predation (Holt *et al.* 2001). This involves a better productivity, which is negatively correlated with body mass. Such selection of smaller organisms has been demonstrated in benthic communities under increasing fish predation pressure (Blumenshine *et al.* 2000). Very small sizes have also been hypothesized to act as a refuge against predation in heterotrophic bacteria or pico-plankton (Jumars *et al.* 1993, Koch 1996, Raven 1998, Boenigk *et al.* 2004). At the opposite, for a certain size of predators, large sizes can also be a refuge for preys (Verity and Smetacek 1996, Jürgens and Sala 2000, Smetacek 2001, Smetacek *et al.* 2004). For instance, larger herbivores suffer lower predation rates in artic tundra relative to smaller ones (Legagneux *et al.* 2014). In plankton communities, the relative proportion of large unicellular algae increases after peaks of grazer rotifers (Gosselain *et al.* 1998). Our model

generates this bimodal distribution for primary producers body mass. A cluster of small producers results from the selection exerted by competition for the resource under herbivory, while a cluster of large producers persists by avoiding herbivory, even if these are less competitive to exploit the resource. Indeed given our interaction rules, large producers are invulnerable since no consumers are sufficiently large to consume them. Therefore, community assembly with our bioenergetic model efficiently reproduces how consumer-resource interactions may shape producers body mass distributions, as commonly found in plankton communities. Two strategies coexist: grazing avoidance at large size and sustaining grazing by better nutrient use at small sizes (Jürgens and Matz 2002, Matz and Jürgens 2003, Thingstad *et al.* 2005).

3.9.3 Effects of the temperature

Our analyses show that distributions of traits crucially depend on temperature. We find a greater proportion of small producers and a lower proportion of small consumers at higher temperatures, with better conversion efficiencies. Many hypotheses have been proposed to explain size reduction with temperature (Daufresne *et al.* 2009, Hilligsøe *et al.* 2011, Gardner *et al.* 2011, Lurgi *et al.* 2012, Hessen *et al.* 2013). The Temperature-Size Relationship (TSR) has been explained by increased metabolic rates at warmer temperatures, with high growth rates leading to smaller adult sizes (Karl and Fisher 2008). Under increased temperatures, cell division is prioritized over cell growth (Van der Have and De Jong 1996). Alternatively under colder temperatures better conversion efficiency allow larger sizes (Neat *et al.* 1995), which maximize the reproductive success accounting for a short reproductive season (Angilletta *et al.* 2004). We do not implement ontogeny or life-history traits in our model, which would produce these direct responses of species size to temperature. But we nonetheless find that temperature also influences indirectly community size structure. This hypothesis was previously proposed by Brose and colleagues (2012), with reference to the modification of interaction strengths (Rall *et al.* 2010) and resource availability (Forster *et al.* 2012; Yom-Tov *et al.* 2006). Temperature increases the biological rates of all species in the same way in our formulation of

bioenergetics models (identical activation energy). Hence, temperature cannot change the competitive hierarchy between species. However, the gain in metabolic activity with temperature decreases the equilibrium density of primary producers (or their carrying capacity when they are grazed), as predicted by metabolic theory (Brown *et al.* 2004, Savage *et al.* 2004, Vasseur and McCann 2005, Meehan 2006). Reduced food availability for small herbivores completely modifies the trophic structure of the community. At warmer temperatures, the smallest producers became invulnerable while the smallest herbivores go extinct. Similarly, warmed experimental communities displayed a shift to autotroph-dominated structures following the loss of top predators and herbivores (Petchey *et al.* 1999, Pounds *et al.* 1999). The emergence of small invulnerable primary producers increases the strength of exploitative competition among invulnerable producers and herbivores (with fewer vulnerable producers too graze). As a side effect, the proportion of large invulnerable producers diminishes because of their lower competitive abilities for resource relative to smaller producers. Many studies have focused on how temperature might change the control type in consumer-resource dynamics (O'Connor *et al.* 2009, Hoekman 2010, Kratina *et al.* 2012). Overall, warming drives a shift in trophic structure via an acceleration of species metabolism: more invulnerable producers on few resources and more herbivores on fewer vulnerable producers. The subsequent strengthening of exploitative competition reinforces the selection pressure towards greater conversion efficiencies.

3.9.4 Future directions for studying trait selection in assembly models

Our work represents a first step in the study of ecological trait selection. We assume several important over-simplifications to focus on basic mechanisms driving food web assembly. Further studies should implement more variability in modeling the dependence of biological rates to body mass and temperature, and integrate the recent findings of the metabolic theory of ecology (Price *et al.* 2012, Humphries and McCann 2014). Notably, species exhibit different activation energies for their biological rates. The balance of ingestion and metabolic rates may have important structural (Petchey *et al.* 2010) and

dynamical (Rall *et al.* 2010) consequences on communities. Moreover, rates potentially respond differently to temperature (Gilbert *et al.* 2014). For instance, increasing temperature may lead to increasing feeding rates but decreasing efficiency, leading to more stable prey-predator dynamics (Vucic-Pestic *et al.* 2011). In the context of assembly process, introducing interspecific variability in allometric constants should reduce the selection pressure exerted on efficiency and body mass by adding dimensions to selection.

Two other important features must be addressed: greater trophic complexity and non-linear dynamics. Trophic complexity includes adding carnivores and top carnivores, and allowing for omnivory, which is common in natural systems (Polis 1991, Diehl 1993) and participates actively to ecosystem stability (Holyoak and Sachdev 1998). We expect trophic complexity to bring important insights on how trait selection cascades over trophic levels. In particular, predation (Chase *et al.* 2009) and the potential decrease of interactions strength (Berlow 1999) may reduce the force of ecological selection. Linear dynamics may provide an acceptable approximation of trait selection for simple systems, such as plankton, but the study of more diverse webs requires integrating non-linear functional responses, which involve additional coexistence mechanisms (Huisman and Weissing 1999, Drossel *et al.* 2004, Gravel *et al.* 2011). The extent to which non-linear dynamics modify trait selection and the impact of temperature on trophic structure remains an open question.

3.9.5 Conclusion

Assembly models are very similar to evolutionary models (Drossel and McKane 2003, Powell and McKane 2009). They both implement a selection process where optimal traits emerge progressively in the community (Lewis and Law 2007). Loeuille and Loreau (2005, 2006) set the bases for studying the diversification of body mass in food webs. Their model assumes an optimal predator body mass for fully exploiting a prey of a given body mass. A size-structured community emerges from the evolution of a single species, with individual variable body masses. Our results show how trophic interactions alone may also drive the selection of body mass and shape community structure, without involving speciation and intraspecific body mass variability.

Our integration of consumer-resource theory to community assembly, using bioenergetic models, gives first theoretical bases to understand in depth how ecological selection structures the distribution of body masses. Further investigations are needed to assess how other aspects of community assembly, such as immigration rate, may affect trait distributions. Faster immigration rates may prevent competitive exclusion of inferior competitors and relax the strength of trait selection. Ultimately, variation in trait distribution driven by ecological selection should affect ecosystem properties (Virgo *et al.* 2006). Since body mass is inversely correlated with productivity, whole ecosystem productivity and biomass production may closely follow the variations of body mass along assembly. In particular, the heavy structural changes we observe with changes in temperature are likely to feedback strongly on ecosystem functioning. Therefore, our study shows that bioenergetic assembly models are exciting tools able to highlight early ecosystem development views (Margalef 1963, Odum 1969, Patten and Odum 1981) with mechanisms linking trait levels to ecosystem functioning (Loreau 2010a, 2010b).

3.10 ACKNOWLEDGEMENTS

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3.11 APPENDIX A – INVASIONS ANALYSIS

Here we present the invasion analysis for a producer trying to invade a tri-trophic food chain at equilibrium (RPH structure). Let us consider a system composed of an herbivore H, feeding upon a producer P_1 having one inorganic resource R, which densities are at equilibrium. We ask whether another producer P_2, initially rare ($P_2 \approx 0$), and sharing the same resource than P_1 and the same herbivore H, can invade the system and exclude P_1. For this, the criteria to be satisfied is:

$$[1] \qquad \left.\frac{dP_2}{dt}\right|_{R^*,P_1^*,H^*,P_2 \ll P_1^*} > 0$$

Taking model 1 as an example, the system can be written:

$$[2] \begin{cases} \frac{dR}{dt} = I - out_R R - \left(a_{P_1}P_1 + \mathbf{a_2P_2}\right)R \\ \frac{dP_1}{dt} = a_{P_1}\phi_{P_1}P_1R - m_{P_1}P_1 - a_HP_1H \\ \frac{dP_2}{dt} = a_{P_2}\phi_{P_2}P_2R - m_{P_2}P_2 - a_HP_2H \\ \frac{dH}{dt} = \left(a_{P_1}P_1 + \mathbf{a_2P_2}\right)a_H\phi_HH - m_HH \end{cases}$$

Since P_2 tends to 0 at invasion, we can approximate the system by deleting the terms containing P_2 in the equation of R and H in the system [1] (in bold and red). Then the invasion criteria becomes:

$$[3] \qquad \left.\frac{dP_2}{dt}\right|_{R^*,P_1^*,H^*,P_2 \ll P_1^*} = a_{P_2}\phi_{P_2}P_2R^* - m_{P_2}P_2 - a_HP_2H^* > 0$$

with: $R^* = \frac{I}{out_R + \frac{a_{P_1}m_H}{a_H\phi_H}}$ and $H^* = \frac{1}{a_H}\left(\phi_{P_1}a_{P_1}R^* - m_{P_1}\right)$ (see Appendix B for the equilibria)

The condition [3] can be written as in Table 5. The conditions for the models 2, 3 and 4 have been derived with the same procedure (results in Table 5). Our interpretation of trait selection is as follows: For the models 1 and 2, the invasion condition involves combinations of several traits in which traits of P_1 cannot be expressed relative to traits of P_2. We derived the direction of trait selection from the form of the invasion condition and from supplementary numerical analyses (Figs. 5 and 6):

For model 1, since the R* is positive by definition, the invasion condition (Table 5) is more easily satisfied if $\phi_{P2}a_{P2}$ is large relative to $\phi_{P1}a_{P1}$ (Fig. 5) and if m_{P2} is small compared to m_{P1}. We conclude that competition should select species with higher conversion efficiency and attack rate, and lower mortality rate.

For model 2, the invasion criteria (Table 5) is more easily satisfied if ϕ_{P2} is large relative to ϕ_{P1} and M_{P2} small compared to M_{P1}. The invader P_2 is more likely to outcompete the resident P_1 if it has the smallest body mass possible and the highest conversion efficiency (Fig. 6a compared to Fig. 6b). We conclude that competition should select species with smaller body mass and higher conversion efficiency.

For models 3 and 4, the species with the smallest body mass wins the competition (Table 5).

Table 5

Invasion conditions for the invasion of the producer P_2, in competition with the resident producer P_1 for the resource R, with an herbivore H feeding on both P_1 and P_2.

Structure	Models	Invasion conditions	R^*
RPH	Model 1	$\phi_{P2}a_2 - \phi_{P1}a_{P1} > \frac{m_{P2} - m_{P1}}{R^*}$	$\frac{I}{out_R + \frac{a_{P1}m_H}{a_H\phi_H}}$
	Model 2	$M_{P2}^{\frac{1}{4}}(\phi_{P2}a_yR^* - a_x) > M_{P1}^{\frac{1}{4}}(\phi_{P1}a_yR^* - a_x)$	$\frac{I}{out_R + \frac{Y_{P1}c_H}{\hat{\psi}_H}}$
	Model 3	$M_{P2} < M_{P1}$	
	Model 4	$M_{P2} < M_{P1}$	

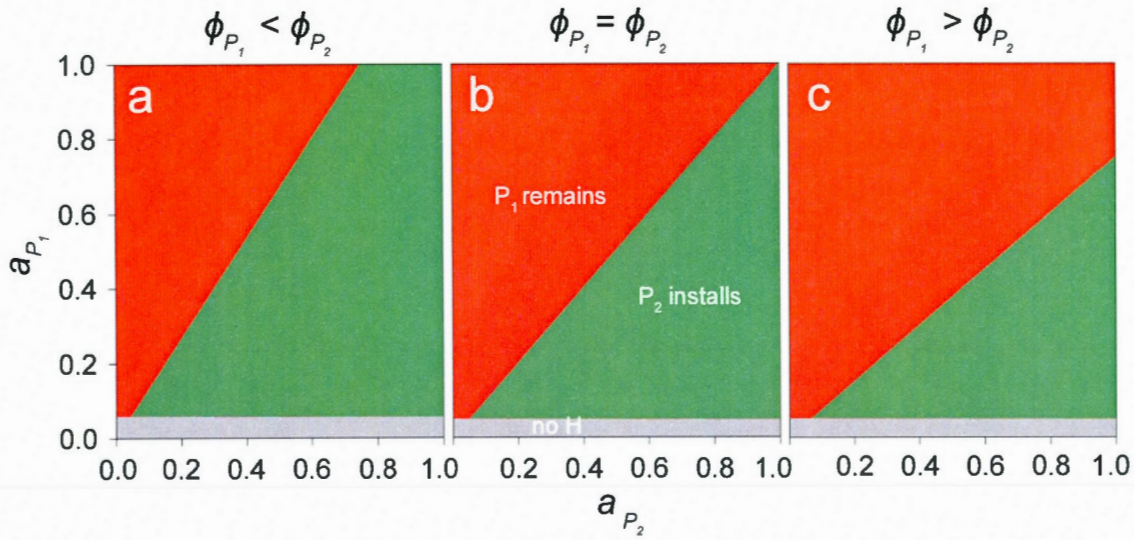

Fig. 5

Outcomes of invasions with model 1 (Lotka-Volterra), attempted by a producer P_2 into a food chain RP_1H when dynamics are at equilibrium, according to the attack rates of P_1 and P_2. P_2 is also a resource for H. Parameter values: $\phi_H = 0.8$, $m_{P1} = m_{P2} = 0.2$; panel a: $\phi_{P1} = 0.6$ and $\phi_{P2} = 0.8$; panel b: $\phi_{P1} = \phi_{P2} = 0.8$; panel c $\phi_{P1} = 0.8$ and $\phi_{P2} = 0.6$. See Table 1 for the other parameter values.

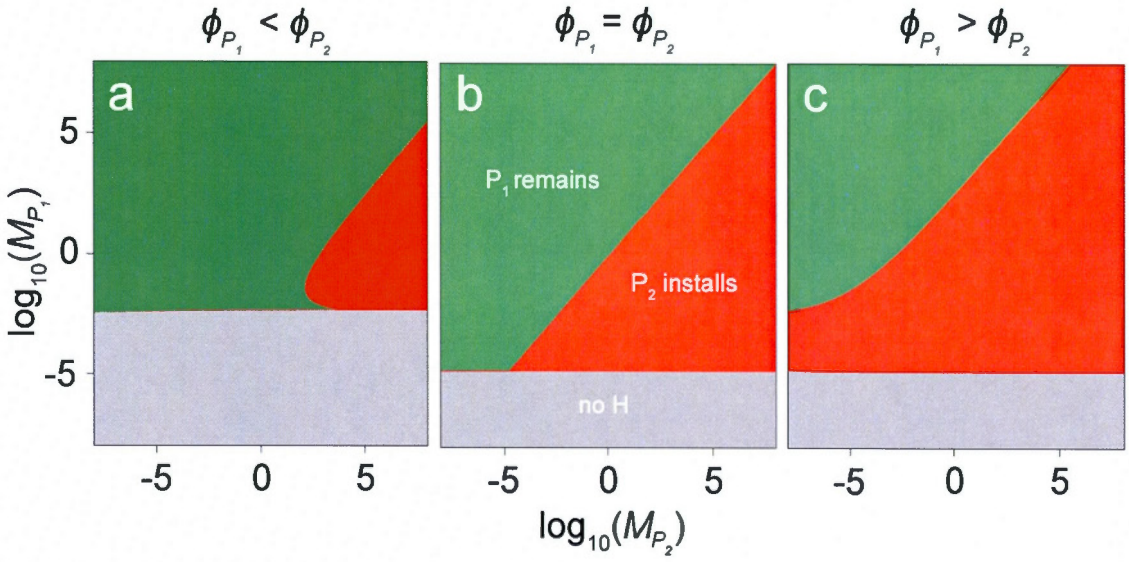

Fig. 6

Outcomes of invasions with model 2 (bioenergetic model with efficiency at the production), attempted by a producer P_2 into a food chain RP_1H when dynamics are at equilibrium, according to P_1 and P_2 $\log_{10}$ of body masses. P_2 is also a resource for H. Parameter values: $\phi_H = 0.8$; panel a $\phi_{P1} = 0.2$ and $\phi_{P2} = 0.8$; panel b: $\phi_{P1} = \phi_{P2} = 0.8$; panel c $\phi_{P1} = 0.8$ and $\phi_{P2} = 0.2$. See Table 1 for the other parameter values.

3.12 APPENDIX B – EQUILIBRIA

Table 6

Equilibria for trophic structures RP and RPH and models 1 to 5. In the bioenergetic models (models 2 to 5) the maximum consumption rate $Y_i = a_{y_{(T_0)}} M_i^{-0.25} e^{\frac{E(T-T_0)}{kTT_0}}$ and the metabolic rate is $X_i = a_{x_{(T_0)}} M_i^{-0.25} e^{\frac{E(T-T_0)}{kTT_0}}$, measured at the reference temperature $T_0 = 20°C$. To simplify the reading we also use the ratio of the biological rates: $c_i = \frac{X_i}{Y_i} = \frac{a_{x_i}}{a_{y_i}}$. This constant is identical for all species within a trophic level. Equilibrium densities are not tractable for structure RPH in model 5.

Structure	Models	R*	P*	H*
RP	Model 1	$\frac{m_P}{a_P \phi_P}$	$\frac{I\phi_P}{m_P} - \frac{out_R}{a_P}$	
	Model 2	$\frac{c_P}{\phi_P}$	$\frac{1}{Y_P}\left(\frac{I\phi_P}{c_P} - out_R\right)$	
	Model 3	c_P	$\frac{\phi_P}{Y_P}\left(\frac{I}{c_P} - out_R\right)$	
	Model 4	$\frac{c_P}{\psi_R}$	$\frac{1}{Y_P}\left(\frac{I\psi_P}{c_P} - out_R\right)$	
	Model 5	$\frac{c_P}{\phi_P}\left(1 + \frac{out_P}{X_P}\right)$	$\frac{1}{Y_P}\left(\frac{I\phi_P}{c_P\left(1 + \frac{out_P}{X_P}\right)} - out_R\right)$	
RPH	Model 1	$\frac{I}{out_R + \frac{a_P m_H}{a_H \phi_H}}$	$\frac{m_H}{a_H \phi_H}$	$\frac{1}{a_H}(\phi_P a_P R^* - m_P)$
	Model 2	$\frac{I}{out_R + \frac{Y_P c_H}{\phi_H}}$	$\frac{c_H}{\phi_H}$	$\frac{1}{Y_H}(\phi_P Y_P R^* - X_P)$
	Model 3	$\frac{I}{out_R + \frac{Y_P c_H}{\phi_P}}$	c_H	$\frac{\phi_H}{Y_H}(Y_P R^* - X_P)$
	Model 4	$\frac{I}{out_R + \frac{Y_P c_H}{\psi_P}}$	$\frac{c_H}{\psi_P}$	$\frac{1}{Y_H}(\psi_R Y_P R^* - X_P)$

3.13 APPENDIX C – TEMPERATURE-DEPENDENCE OF P*

Producer equilibrium density P* suffering no herbivory (RP structure) usually decreases with temperature (Table 4, models 2 to 4). When body mass – independent losses are added (model 5), the producer equilibrium density P^* is:

$$[4] \qquad P^* = \frac{1}{Y_P}\left(\frac{I\phi_P}{c_P\left(1+\frac{out_P}{X_P}\right)} - out_R\right)$$

with $Y_P = a_{y_{(T_0)}} M_P^{-0.25} e^{\frac{E(T-T_0)}{kTT_0}}$ and $X_i = a_{x_{(T_0)}} M_i^{-0.25} e^{\frac{E(T-T_0)}{kTT_0}}$ (values and symbols explained in Table 2). The derivative is too complex to be written, but numerical analyses show that, for the range of temperature we consider (0-40°C), the relationship between P^* and temperature can be either negative (Fig. 7a) or non-linear (Fig. 7b), depending on producer's traits.

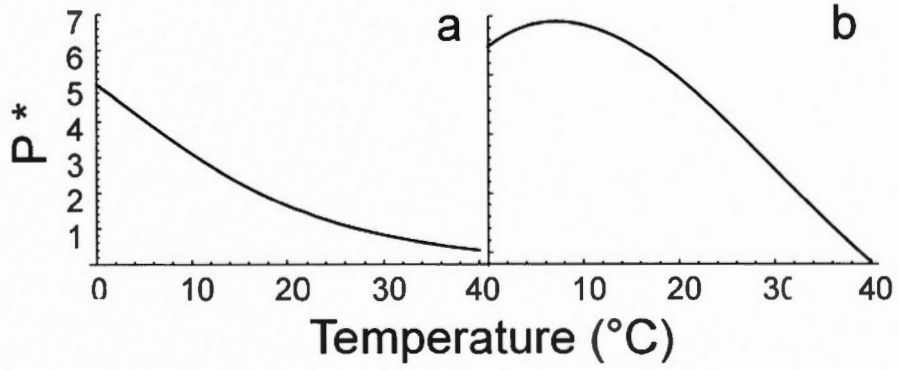

Fig. 7

Relationship between producer equilibrium density and temperature with the model 5 (with output independent from the metabolism), and without the herbivore, for two contrasted body masses of the producer, M_P. Panel a: $M_P = 0.01$; panel b: $M_P = 100$. Producer conversion efficiency, $\phi_P = 0.01$ for both panels. Values of other parameters are found in Table 2.

3.14 APPENDIX D – TEMPERATURE AND CONSUMER CRITICAL EFFICIENCY

When temperature increases, the maintenance of herbivores requires greater r conversion efficiencies. In the case of one herbivore H feeding on one producer P, the critical herbivore conversion efficiency (i.e. the efficiency limit above which the herbivore has enough food to maintain) depends on producer body mass and conversion efficiency (Fig. 8). The producer traits parameter space where no herbivore can maintain (i.e. which would require the critical herbivore conversion efficiency to be more than 1) increases with temperature (Fig. 8, grey area).

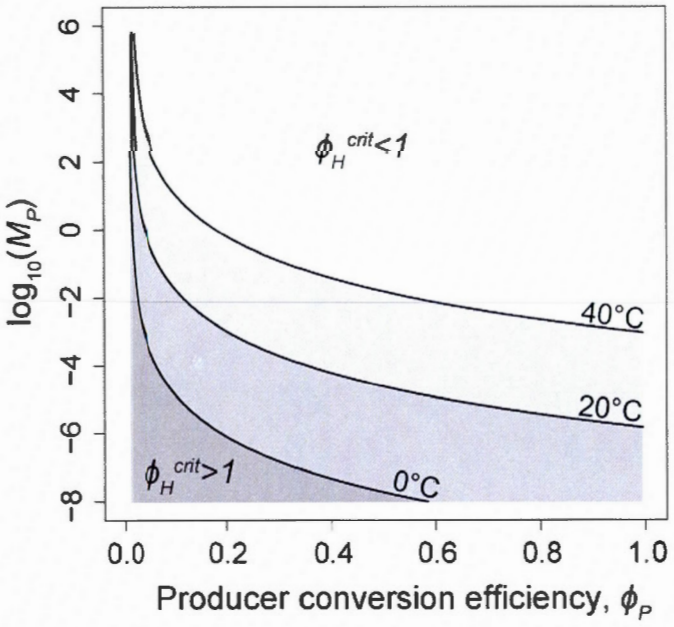

Fig. 8

Isoclines where the critical conversion efficiency of the herbivore, ϕ_H^{crit} , is equal to 1, according to the conversion efficiency and the log of the body mass of its single prey, and for temperatures 0, 20 and 40°C. ϕ_H^{crit} is defined as the efficiency limit above which the herbivore has enough food to maintain. Since, the maximal ϕ_H is 1, the grey area where ϕ_H^{crit} is greater than 1 is the parameter space of the producer traits for which no herbivore can install.

CHAPITRE 4
ASSEMBLAGE DES ÉCOSYSTEMES (2): EFFET DU TIMING D'ASSEMBLAGE

4.1 TITRE

Le timing de l'assemblage structure la diversité et le fonctionnement de réseaux trophiques théoriques

4.2 RÉSUMÉ

Les écosystèmes sont soumis à des perturbations récurrentes. Les conséquences potentielles incluent que la re-colonisation par les espèces peut mener le développement des écosystèmes vers des états stable alternatifs en fonction de contingences historiques, ce qui défie la capacité des écologistes à prédire leurs réponses aux perturbations. La théorie de l'assemblage des communautés a focalisé ses efforts sur les effets de priorités, et l'évaluation du rôle que joue la séquence d'espèce (ordre d'arrivée) dans les propriétés des communautés finales. Le timing de l'assemblage (temps relatifs entre les évènements de colonisation) est aussi une source évidente de variabilité dans le développement des systèmes naturels. Bien qu'il soit probable que le timing puisse aussi faire diverger les trajectoires d'assemblage, son rôle a encore été peu étudié.

Nous développons un modèle bioénergétique d'assemblage de réseaux trophiques pour examiner comment le timing d'assemblage affecte la diversité et le fonctionnement des réseaux trophiques. Nous testons par des expériences numériques l'effet que produisent différents aspects du timing d'assemblage sur les réseaux trophiques (vitesse d'assemblage, agrégation : nombre de colonisateurs simultanés), indépendamment de la séquence d'espèces. Parce que les effets de priorités peuvent dépendre de la réponse fonctionnelle

des espèces, nous comparons pour chaque expérience des séries de simulations avec des réponses soit linéaires, soit non-linéaires.

Nous trouvons que la sensibilité des réseaux trophiques aux effets de contingences historiques induit par le timing dépend fortement de la linéarité des dynamiques. Avec des dynamiques linéaires, des vitesses d'assemblages plus rapides augmentent la richesse finale en espèce et le plus fort cumul de biomasse est obtenu pour des vitesses intermédiaires, qui permettent une plus grande complexité trophique. Au contraire, avec des dynamiques d'interaction non-linéaires, les réseaux trophiques sont relativement peu affectés par la vitesse d'assemblage, mais sont sensibles à l'agrégation des colonisations. Nous expliquons ces variations de diversité et de fonctionnement par l'impact des caractéristiques de l'assemblage sur la distribution des masses corporelles spécifiques du réseau. Par là, notre étude contribue à poser de nouvelles bases pour intégrer les travaux menés séparément sur l'assemblage des communautés et la théorie de la succession.

Cet article intitulé « The timing of species assembly shapes the diversity and functioning of simulated food webs » a été co-rédigé par mes directeurs de thèse Dominique Gravel et Nicolas Mouquet, la chercheuse Sonia Kéfi et moi-même. Le manuscrit est en préparation pour être soumis pour publication dans la revue *Ecology*. Dans ce but, la discussion a encore besoin d'être épurée dans le style, et approfondie concernant l'effet des réponses fonctionnelles non-linéaires, et la comparaison avec la littérature empirique et la théorie de la succession.

En tant que première auteure, j'ai réalisé la recherche bibliographique, l'élaboration du modèle et le design des simulations, la programmation du modèle, l'analyse des résultats ainsi que l'essentiel de la rédaction. Dominique Gravel, dernier auteur, et moi-même avons élaboré la problématique et le choix du modèle. Nicolas Mouquet, 2nd auteur, et Dominique Gravel ont participé à la rédaction. Sonia Kéfi, 3ème auteure, a participé à la résolution des problèmes techniques sur le modèle, ainsi qu'à la rédaction.

J'ai présenté une partie des résultats de cette étude lors d'une session orale de la 99ème conférence annuelle de la Société Américaine d'Écologie (ESA), en août 2014 à Sacramento.

4.3 TITLE

The timing of species assembly shapes the diversity and functioning of simulated food webs

4.4 ABSTRACT

Ecosystems are submitted to recurrent disturbances. Alternative successional trajectories are susceptible to happen because of historical contingencies occurring as species re-colonize ecosystems, challenging ecologists' ability to predict ecosystem responses to disturbances. Community assembly theory has mainly focused on the role of the order of species arrival. The timing of assembly is also a source of variability in the development of natural systems. Although it is likely to induce divergent assembly trajectories, it has still been scarcely studied. We develop a bioenergetic food web assembly model to investigate how the timing of assembly affects the diversity and functioning of food webs. We perform numerical experiments to test the effect of the rate and aggregation of colonization events, independently of the species sequence. Because priority effects may depend on functional responses, we contrast simulations using linear and non-linear responses. We find that the sensitivity of food webs to timing-induced historical contingencies strongly depend on the type of functional response. Faster assembly rates increase final richness for linear response, but highest biomass is obtained for intermediate assembly rates, which allow a greater trophic complexity. By contrast, with non-linear functional responses, food webs are relatively unaffected by assembly rates but they are sensitive to the number of simultaneous colonizers. We explain the variations in diversity levels and ecosystem functioning by the impact of assembly characteristics on the resulting distributions of body masses in the assembled food webs. Overall, our study sets up some bases to bridge the gap between community assembly and succession theory.

4.5 KEYWORDS

Community assembly, bioenergetic model, ecosystem functioning, functional response

4.6 INTRODUCTION

All ecosystems are submitted to disturbances, of greater or lower intensity, more or less frequently (Attiwill 1994, Turner *et al.* 1998, Borics *et al.* 2013). After important disturbances (e.g. storms, fire, volcanic eruption), ecosystems re-develop with the progressive re-colonization of the site by species. Succession theory proposes that the assembly process follows a deterministic sequence (Clement 1916, Tansley 1935, Margalef 1963, Odum 1969, Connell and Slatyer 1977), but historical contingencies driving the arrival of species may make the assembly deviate from its expected trajectory (Gleason 1927, Diamond 1975, Jenkis and Buikema 1998, Almany 2003, Fukami and Morin 2003, Fukami *et al.* 2005). A mixture of deterministic and stochastic events finally shapes the resulting communities (Belyea and Lancaster 1999, Young *et al.* 2001, Briske *et al.* 2003). Our study specifically addresses the role of the timing of assembly in structuring community composition and ecosystem functioning. We define the timing as the relative times at which the colonization events occur during the assembly process.

Community assembly proceeds according to successive development phases, which may overlap. First, early colonizers establish and grow. Competition takes place among primary producers following a decrease in resource availability. Their establishment creates niches for further colonization by herbivores and carnivores. Herbivory and predation then after regulate the growth of basal species. Gradually, complex indirect interactions set up in the community (Wootton 1994, 2002, White *et al.* 2006). For instance, the arrival of a productive species may negatively affect the population of another one through apparent competition (Holt and Lawton 1994, Holt *et al.* 2001) by benefiting the growth of a common generalist predator and inducing "hyperpredation" (Courchamp *et al.* 2000). Conversely, a weak competitor may persist thanks to a specialist predator feeding on its

competitors (Paine 1974, Adams *et al.* 2003). Some species get extinct and are replaced. Finally, if no novel disturbance happens, the ecosystem may reach a stationary state with constant diversity, community structure and biomass production, among other properties (Margalef 1963, Odum 1969).

Succession theory has been one of the corner stones of ecology (Young *et al.* 2001). It has long been studied, notably in terrestrial plant communities (Egler 1954, Connell and Slatyer 1977, Pickett *et al.* 1987, Huston and Smith 1987). Common features were identified across ecosystems (Lake *et al.* 2007). However, in nature, species may arrive in different orders and at different paces. Some colonizers may arrive simultaneously, like plants growing from local seed banks after a fire, or species arriving through storms. Others may arrive successively because of differential dispersal abilities and distance from the seed source. These sources of variability are likely to affect the trajectory of ecosystem development.

While succession theory focus on convergent patterns in ecosystem development, community assembly theory rather assesses the role of historical contingencies in producing divergent assembly trajectories (Young *et al.* 2001). In a region, the assembly of the same set of species may result in very different communities (Chase 2003a), which challenges our capacity to predict their response to disturbances and their recovery dynamics. Models as well as experiments demonstrated that, in some cases, the order in which species arrive in the ecosystem modifies the diversity, composition or functioning of the final community (Drake 1990, 1991, Law and Morton 1993, Lockwood *et al.* 1997, Fukami and Morin 2003, Fukami 2005, Fukami *et al.* 2007, Jiang and Patel 2008, Olito and Fukami 2009, Fukami *et al.* 2010, Dickie *et al.* 2012).

Several mechanisms can make early colonizers change the success probability of further colonizers, resulting in "priority effects" (*sensu* Alford and Wilbur 1985). We can categorize these mechanisms in three types involving (1) strong competitive interactions, (2) non-linear consumer-resource dynamics, or (3) modifications of the environment. First, classical Lotka-Volterra competition models predict that the outcome of a pair-wise

competition depends on initial densities if interspecific competition exceeds intraspecific competition (Case 2000). When species strongly interfere, for instance between some reefs fishes, the first arrived may develop such that it acquires a competitive advantage on the next colonizers (Almany 2003). Similarly, early colonizers may preempt a limited resource such as space or light for plants and prevent the set up of later arrivers (Körner *et al.* 2008). Other resources are not pre-emptible. In that case, consumer-resource theory suggests that a species able to deplete an inorganic resource below the minimal requirement of a competitor having the same niche, would exclude it whatever their relative densities (Gause 1934, Tilman 1977, 1980). In that case, the outcome of exploitative competition is purely deterministic. The second type of mechanisms involves non-linear dynamics: depending on the initial density of a prey at the arrival of its predator, a predator-prey system may either drop into an overexploited state or reach an abundant steady state (Noy-Meir 1975, May 1977, Van de Koppel and Rietkerk 2000, Feng *et al.* 2006). In the context of assembly, the outcome may therefore vary according to the relative abundances of prey and predator at the time of their encounter (Chase 2003b). Third, while growing, early-arrived species may modify the environment (Hobbs 1996) such that it will favor or prevent the further set up of next arrivers. Beyond the emblematic examples of ecosystem engineers (Jones *et al.* 1994, Hastings *et al.* 2007) of beavers building dams that flood plains (Naiman *et al.* 1994, Wright *et al.* 2002), or legumes fixing nitrogen (Pugnaire *et al.* 1996), most plants develop specific microbial communities in the soil (Bever 2003, Pringle *et al.* 2009) or some algae excrete toxins to conserve their dominance (Legrand *et al.* 2003). Cascade effects within the resident species network may then accentuate the trajectory divergence initiated by priority effects. For instance, unstable configurations, such as predators whose offspring are consumed by their prey, may disappear thanks to changes in relative abundance (Walters and Kitchell 2001), or a generalist predator arrived first may prevent the set up of its potential resource species (Louette and De Meester 2007), depriving next colonizers of this essential resource. Finally, distal causes of priority effects comprise greater regional diversity (Law and Morton 1996, Fukami 2004, Jiang *et al.* 2011), greater fertility (Chase

2010) or greater similarity of species (Peay *et al.* 2012, Tan *et al.* 2012, Suding *et al.* 2013). All these conditions contribute to increase the probability of assembly divergence.

To explain and assess historical contingency effects on communities, community assembly theory has focused on the order of species arrival (above section). However, other characteristics of the assembly process, such as the relative times at which species arrive in the ecosystem, are likely important for food web assembly. For instance, priority effects would develop only if early colonizers have enough time to grow (getting a competitive advantage) or to modify the environment in a significant way before the arrival of the next colonizers. Similarly, with a fast assembly rate (short time between two colonizations), some indirect interactions, such as predation regulation of competitors, may prevent the competitive exclusion of species less efficient at exploiting the resource. As a third example, with non-linear dynamics, if a predator arrives too fast after the installation of its prey, it is likely that the interaction would stabilize in an overexploited state (low density of both predator and prey), whereas, if it arrives later, the same interaction may stabilize in an abundant state (May 1977). Such variations in relative abundances due to assembly rate may also feedback on other interactions in the food web (Walters and Kitchell 2001). Overall, the time between species arrivals may strongly influence the set up of complex indirect interactions and the persistence of weak competitors and hence the final diversity.

Usually, species-centered models of community assembly make the simplifying assumption that the community reaches equilibrium between two colonizations (Post and Pimm 1983, Law and Morton 1993, 1996, Wilmers *et al.* 2002, Lehmann-Ziebarth and Ives 2006, Virgo *et al.* 2006). In nature however, species may arrive in the ecosystem on a time depending on their initial distance from the site (Turner et al. 1998, Jacquemyn et al. 2001), their dispersal ability or mobility (Ehrlen and Eriksson 2000), and environmental factors such as wind, susceptible to aggregate species arrivals (Caceres and Soluk 2002). Three interrelated aspects shape the timing of species assembly (successive species arrivals along time): (1) the assembly rate (time between two successive colonizations); (2) the variability of this rate along the assembly, because species arrivals are likely to not be regular in nature; (3) the aggregation, because species may arrive in group, by chance or through

storms or floods (Walker and Neris 1993). We expect these aspects of assembly timing to affect the composition and structure of the resulting communities via the mechanisms described above, although very little is known about what these effects are.

To study the effects of assembly timing on food webs, we propose to combine the sequential colonization process of classical assembly models to recent food web models. We focus on food web assembly where divergent trajectories emerge solely from trophic interactions, excluding deliberately the implementation of feedbacks on the environment ("niche construction" *sensu* Odling-Smee *et al.* 2013) despite their known role in primary succession (*e.g.* facilitation mechanisms by legumes, Huston and Smith 1987). The only facilitation mechanism we consider is the niche construction that results from the installation of species becoming a resource for others.

Assembly models usually represent community dynamics by generalized Lotka-Volterra equations with linear dynamics (Case 1990, 1991, Law and Morton 1993, 1996, Lehmann-Ziebarth and Ives 2006, Virgo *et al.* 2006). We implement bioenergetic constraints set by the metabolic theory (Yodzis and Innes 1992, Brown *et al.* 2004). Like in the most recent food web models, specific body mass is used to link explicitly trophic flows to species metabolism (Brose *et al.* 2006b, Berlow *et al.* 2009). This is a particularly powerful framework to relate community composition and structure to ecosystem functioning through species traits (Woodward *et al.* 2005). Furthermore, since multistability is a particular feature of non-linear dynamics, we suspect that priority effects and assembly divergence would strongly depend on the functional response considered. Therefore we compare the food web structure emerging from assembly using either linear functional responses (like in classical assembly models) or non-linear functional responses (like in recent food web models), and their sensitivity to historical contingencies.

Our main objective is to study the effects of assembly timing on food web diversity and properties. We structure our study in three related questions: (Q1) How do the different aspects of assembly timing (namely assembly rate, variability of assembly rate and aggregation) affect the diversity of the resulting food webs, regardless of the species

sequence? (Q2) How do these potential contingent effects depend on the linearity versus non-linearity of the species functional responses? (Q3) What are the consequences of assembly timing on the structure and the functioning of assembled food webs?

4.7 METHODS

We run numerical experiments for which we vary several aspects of the assembly timing while keeping constant the species sequence. We contrast simulations of linear versus non-linear functional responses. We compare the diversity of the assembled food webs to evaluate the role of assembly timing in producing alternative stable states. We also examine the resulting consequences on trait composition (body mass), community structure (trophic groups, connectance) and ecosystem functioning (biomass).

4.7.1 Model structure

We use a bioenergetic consumer-resource model where the basal level is constituted by ten classes of inorganic resources R_i representing niches for primary producers. Producers are allowed to consume 1 to 3 consecutive basal resources. The consumers feed either on producers or on consumers. Consumer body mass is drawn from a lognormal distribution fitted on empirical data (data in Brose *et al.* 2005) and determines its diet. The position of all species on the niche axis is the log10 of their body mass. The diet optimum of a consumer of a given body mass is provided by the linear empirical relationship between prey and predator body masses (Brose *et al.* 2006a). The boundaries of a consumer's diet are given by the 10% and 90% quantile regressions (Gravel *et al.* 2013). Consumers eat all species whose body mass fall into their diet range (niche model structure, Williams and Martinez 2000) We assume producers to have an average body mass lower than the one of consumers (see Table 1 for values of their lognormal distribution). The model describes the fluxes of nutrients among food web compartments and we assume species biomass B_i to be directly proportional to nutrient content. The variation through

time of the nutrient density in the food web is described by a set of ordinary differential equations:

$$\frac{dR_i}{dt} = I - eR_i - \sum_j Y_j B_j F_{ji}$$

$$\frac{dB_i}{dt} = \sum_j \varepsilon_i Y_i B_i F_{ij} - X_i B_i - \sum_j Y_j B_j F_{ji}$$

The basal resource R_i is supplied by a constant external inflow I (*e.g.* weathering) and loses nutrients from interaction-independent processes (*e.g.* leaching) a constant rate e and from consumption by producers. Species i gains biomass B_i from the consumption of other species and resources (producers), according to a maximum consumption rate Y_i. The realized uptake on compartment j is modulated by the functional response F_{ij}, which can be either linear: $F_{ij} = \omega_i B_j$, or non-linear: $F_{ij} = \omega_i B_j^{h_i} / \left(B_0^{h_i} + \sum_k \omega_i B_k^{h_i}\right)$. The preference of species i for each of its n resources is uniform ($\omega_i = 1/n$). Non-linear functional responses are shaped by the half saturation constant B_0 and the hill exponent h_i, which is randomly drawn from a uniform distribution between 1 and 2 (as in Brose *et al.* 2006b, Berlow *et al.* 2009). This makes the species functional responses vary from type 2 to type 3. Species i converts a proportion ε_i of the uptake into new biomass (conversion efficiency). It loses biomass either from catabolism according to its metabolic rate X_i, or from consumption by other species (herbivory or predation). The biological rates Y_i and X_i are written as an inverse exponential function of the body mass, M_i, as proposed by the metabolic theory (Brown *et al.* 2004): $a_z M_i^{-0.25}$, with a_z the constant of the allometric relationship between the rate measured and the body mass. For the sake of simplicity, we assumed identical allometric constants for the different species of either producers or consumers (see Table 1).

Table 1: Symbols and values of the parameters used for the simulations

Symbols	Description	Dimensions	Values
R_i, B_i	Densities* of the compartments: the inorganic resource, or the species (Biomass) i	$M.L^{-2}$	-
I	Input of inorganic nutrient	$M.L^{-2}.T^{-1}$	1
e	Output rate of the inorganic resource	T^{-1}	0.1
M_i	Specific body mass of species i *(C: data from Brose et al. 2005)*	M	C: $log\mathcal{N}(-1.67, 6.25)$ P: $log\mathcal{N}(-2.50, 6.25)$
ε_i	Conversion efficiency of species i Normal distributions for P and C of autotroph-based and detritivore webs in this order.	*dimensionless*	P_{auto}: $\mathcal{N}(0.85, 0.20)$ C_{auto}: $\mathcal{N}(0.70, 0.20)$ P_{det}: $\mathcal{N}(0.60, 0.20)$ P_{det}: $\mathcal{N}(0.70, 0.20)$
a_x	Allometric constant for the metabolic rate. Values for producers, invertebrates and vertebrate ectotherms, respectively	$T^{-1}.M^{1/4}$	$\{0.138, 0.314, 0.880\}$ (Brose et al. 2006b)
a_y	Allometric constant for the maximum consumption rate. Values for producers, invertebrates and vertebrate ectotherms, respectively	$T^{-1}.M^{1/4}.(M.L^{-2})^{-1}$	$\{1, 2.512, 3.520\}$ (Brose et al. 2006b)
X_i	Metabolic rate of species i	T^{-1}	$a_x M_i^{-0.25}$
Y_i	Maximum consumption rate of species i	$T^{-1}.(M.L^{-2})^{-1}$	$a_y M_i^{-0.25}$
ω_i	Preference of species i for each of its n resources	*dimensionless*	$1/n$
F_{ij}	Functional response of species i consuming compartment j	T^{-1}	–
B_0	Half saturation constant	$M.L^{-2}$	0.5
h_i	Hill exponent (non-linear functional responses) of species i	*dimensionless*	$\mathcal{U}[1,2]$

* *Note that density means stock or biomass by unit of surface, not abundance of individuals.*

4.7.2 Assembly process

Simulations start by creating a pool of 2500 species, and selecting at random the order in which they arrive (figure 1). We will keep strictly the same species sequence while we vary assembly timing. Species have the same probability to be a primary producer or a consumer. Their traits (body mass M, conversion efficiency ε and hill exponent h) are drawn at random from the distributions given in Table 1.The ecosystem is initially empty

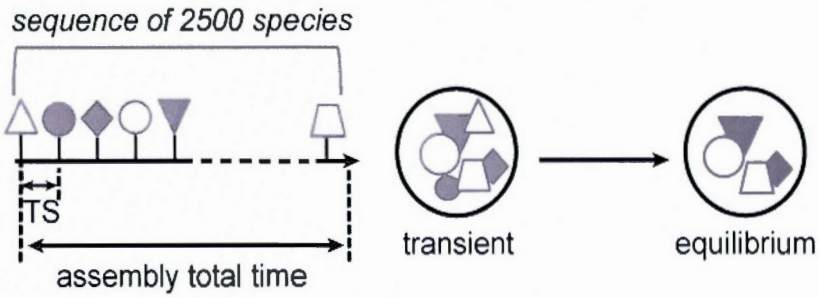

Fig. 1 Simulation algorithm – the assembly process
We create a pool of 2500 species (grey shapes) and select at random the order in which these species will colonize the ecosystem (black circle). The time separating 2 assembly steps (i.e. colonization events) is called timestep TS. The sum of all the timesteps is the total time of the assembly process. We record the final food web after the last timestep constituting the assembly process (transient food web). We then run the dynamics until equilibrium, we remove the extinct species, and we record also this equilibrium food web.

and species try to install in the order determined by the species sequence with an initial low density (10^{-4}).

A colonization event corresponds to an *assembly step*. The *timestep TS* is defined as the number of time units between 2 assembly steps (figure 1). The sum of all timesteps represents the *assembly total time*. The assembly rate is the number of colonization event by unit of time. For each assembly step we add the colonizer (-s) in the ecosystem and compute the new interaction matrix. We then run the numerical integration with the

algorithm Runge-Kutta Kash Carp of the gsl 1.15 library (Galassi *et al.* 2011) during TS number of integration steps. We consider a species extinct, and remove it from the ecosystem when its density is below a threshold of 10^{-6} units of biomass (far below the expected equilibria). At the end of the assembly, after the run of the last TS, we record the characteristics of the *transient food web* (richness, species traits and biomasses) and run the dynamics until equilibrium to remove all the transient species. We detect equilibria by comparing averages on two successive windows of 500 integration steps (some simulations have oscillating dynamics). Stationary state is reached when the absolute difference for each compartment between successive windows is less than 10^{-11}. After removing the extinct species, we finally record the characteristics of this *equilibrium food web*.

4.7.3 Numerical experiments

We design 3 numerical experiments to test the effects of the different aspects of assembly timing on final food web composition and properties (fig. 2). For each experiment, we run 200 simulations with either linear or non-linear functional responses. And for each simulation within an experiment, we keep the same species sequence, while varying the aspects of assembly timing.

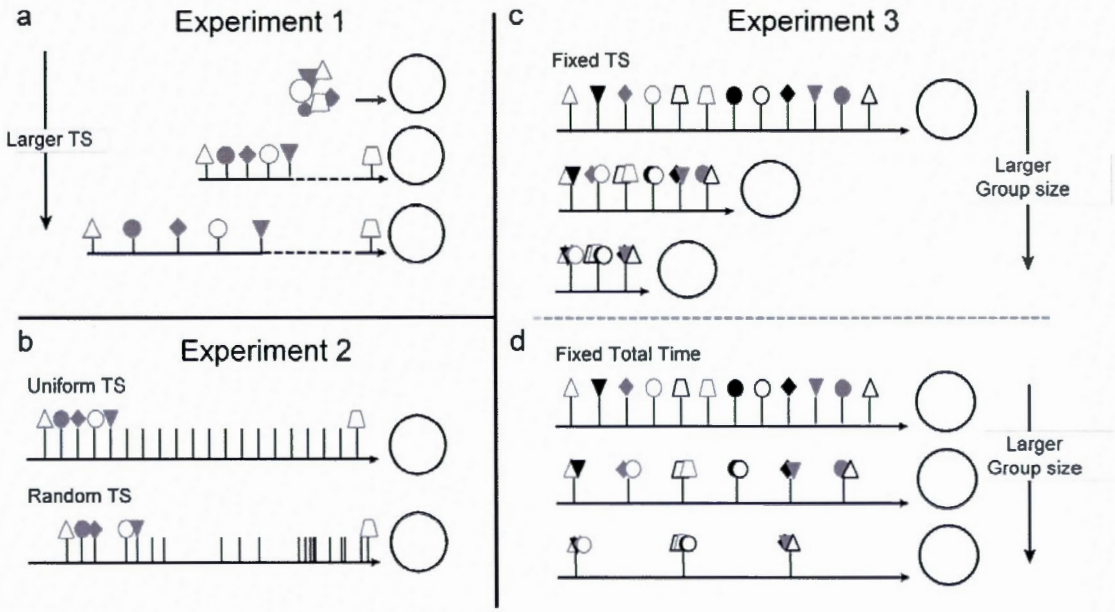

Fig. 2 Design of numerical experiments

Black and grey small shapes represent different species. The length of the horizontal arrows illustrates the total time of an experiment. Vertical lines along the assembly sequence represent the colonization events, and the time separating 2 colonization events is the timestep TS. Panel (a) shows the design of experiment 1, for which we vary the timestep TS, starting from a simultaneous assembly. Total time of assembly increases with TS. Panel (b) shows the design of experiment 2, for which we contrast simulations with Uniform TS and Random TS, keeping the same total time, and the same number of colonization events. Panels (c) and (d) show the design of experiment 3, for which we vary the aggregation, that is the number of species trying to colonize the ecosystem in the same time (group size). We contrast a version where TS is fixed and total time decreases with aggregation (c), and a version where total time is fixed and TS increases with aggregation (d). Within all design (a to d) we keep the same species in the same order among treatments.

In experiment 1 (fig. 2, panel a) we change the assembly rate by varying the timestep TS from 0 (simultaneous assembly) to a case for which we reach equilibrium at each assembly step: $TS = \{0, 2, 5, 10, 50, 100, EQ\}$. Larger TS slows down the assembly rate.

In experiment 2 (fig. 2, panel b) we test the effect of variable assembly rates. We contrast simulations with regular or irregular arrival of species, leading to uniform versus

random TS. For random TS, we select at random from a uniform distribution the location of 2500 events in a sequence starting from 0 and ending at TS. Then the 2500 colonizations occur according to the successive moments sorted in increasing order along assembly time. We run pairs of simulations with uniform *versus* random TS for all the TS of Experiment 1.

In experiment 3 (fig. 2, panels c and d), we change the aggregation by varying the group size, i.e. the number of species that arrive in the ecosystem during a single assembly step: $Group\ size = \{1, 2, 4, 10, 20, 50\}$. The total number of species in experiment 3 is 2400, instead of 2500, because we also tried multiple of 3 sizes in preliminary simulations. Note that, despite aggregation, species arrive in the same order. We contrast simulations where either TS is fixed and total assembly time decreases with aggregation (fig. 2, panel c), or total assembly time is fixed and TS increased with aggregation (fig. 2, panel d). This two-side design isolates the effect of aggregation from assembly rate while keeping constant the number of species arriving in the ecosystem. For fixed TS we use an intermediate timestep: $TS = 20$. The qualitative results are not different for other TS. For fixed total time we use $Total\ time = 4800$, such that at intermediate aggregation ($Group\ size = 10$) the assembly proceeds through the same $TS = 20$ for both sides of Experiment 3.

4.8 RESULTS

We first assess the historical effects due to assembly timing by comparing the richness of the final food webs within each of the 3 experiments. This is a conservative approach since richness is a coarse property of community composition. We then go further for experiment 1 by examining the impact of assembly rate on the body mass distribution, the trophic structure and the biomass of the final food webs.

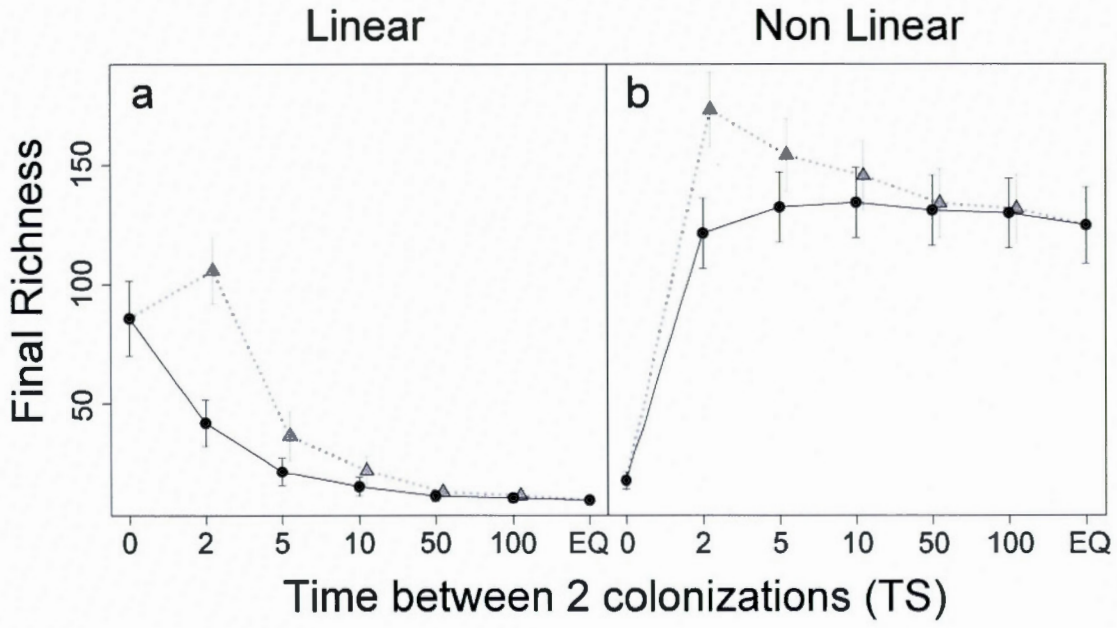

Fig. 3 Richness of food webs according to the time between colonization events (TS) In panel (a) we use linear functional responses, in panel (b) non-linear functional responses. "EQ" means that the equilibrium is reached between each colonization event. Points are means over 200 replicated simulations. Bars give the standard deviation. Grey triangles indicate transient food webs and black circles indicate equilibrium

4.8.1 Experiment 1: Assembly rate ~ Richness

The effect of assembly rate on food web richness depends radically on the type of species functional responses. First, we find that final richness at equilibrium (fig. 3, black points) decreases with increasing timestep (TS) with linear functional responses, whereas assembly rate has no significant effect on richness with non-linear functional responses. Second, a non-linear functional response allows maintaining a much higher final richness than can do a linear functional response, regardless of the TS (except in the case of simultaneous assembly, fig. 3b, $TS = 0$). Third, simultaneous assembly ($TS = 0$) is a special case, for which almost no consumer manages to persist owing to the small initial density of their resources (see figs. A and C for an illustration). It results in a very low richness of primary producers, close to the number of basal inorganic resources, with a

non-linear functional response. On the contrary, a higher richness is reached with a linear functional response (fig. 3a). However, biomasses of consumers indicate they are close to extinction (Appendix figs. A3, C3), suggesting that the dynamics for simultaneous assembly are so slow that despite our conservative method to detect steady state, the communities had not reached steady state. Finally, with both types of functional responses, transient food webs recorded at the end of the assembly process display greater richness than at equilibrium (fig. 3, triangles and dotted lines). However, the richness difference between transient and equilibrium food webs disappears with increasing TS.

4.8.2 Experiment 2: Variability of the assembly rate ~ Richness

The variability of the assembly rate does not impact the final richness in average, but

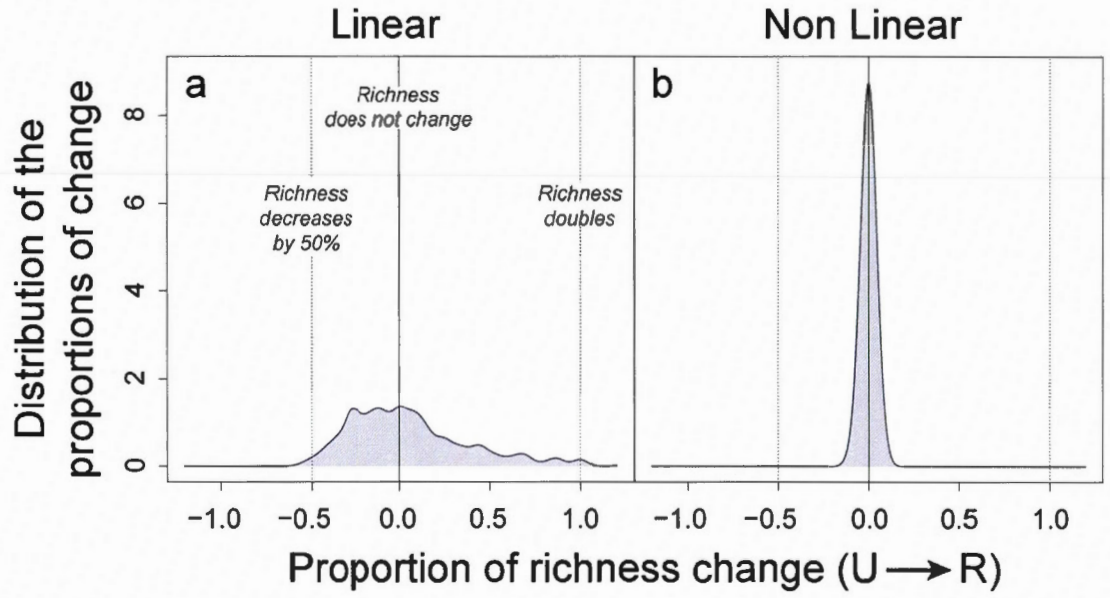

Fig. 4 Changes in final richness with variable assembly rates

Distribution of the proportions of change in final richness for the same species sequence assembled either with uniform (R_U) or random (R_R) timesteps, and using either linear (a), or non-linear functional responses (b). The proportion of change is computed with $(R_R - R_U)/R_U$. We show results for an intermediate timestep ($TS = 10$) but results are similar for $TS \in \{2, 5, 50, 100, EQ\}$.

may affect it for particular sequences with the linear functional response. To evaluate the effect of assembly rate variability we plot the distributions of the proportion of change between the richness of food webs assembled with uniform TS (R_U) *versus* random TS (R_R): $(R_R - R_U)/R_U$, for the same species sequence. Figure 4 shows the case of an intermediate TS ($= 10$), but the results are similar for other TS (data not shown). The median is always, or very close to, zero. With linear functional responses (fig.4a), the distribution is more dispersed than with non-linear functional responses (fig.4b). This dispersion shows that historical effects due to variable assembly rates may be strong for some particular sequence. The direction of richness change is idiosyncratic. However, most of the values are close to zero.

4.8.3 Experiment 3: Aggregation ~ Richness

Richness at equilibrium increases with aggregation in the case of a linear functional response and decreases with aggregation in the case of non-linear functional response (figs. 5a and 5b, black lines). A loss of consumers with aggregation is observed for both cases (Appendix, fig. D). When the total length of the assembly process is held constant (figs.5c and 5d, black lines), increasing aggregation has no effect on final richness regardless of the functional response, except a slight decrease for strong aggregation. In all cases, transient food webs display greater richness than at equilibrium (fig.5, dotted lines). The difference with equilibrium richness is stronger for fixed TS and increased aggregation.

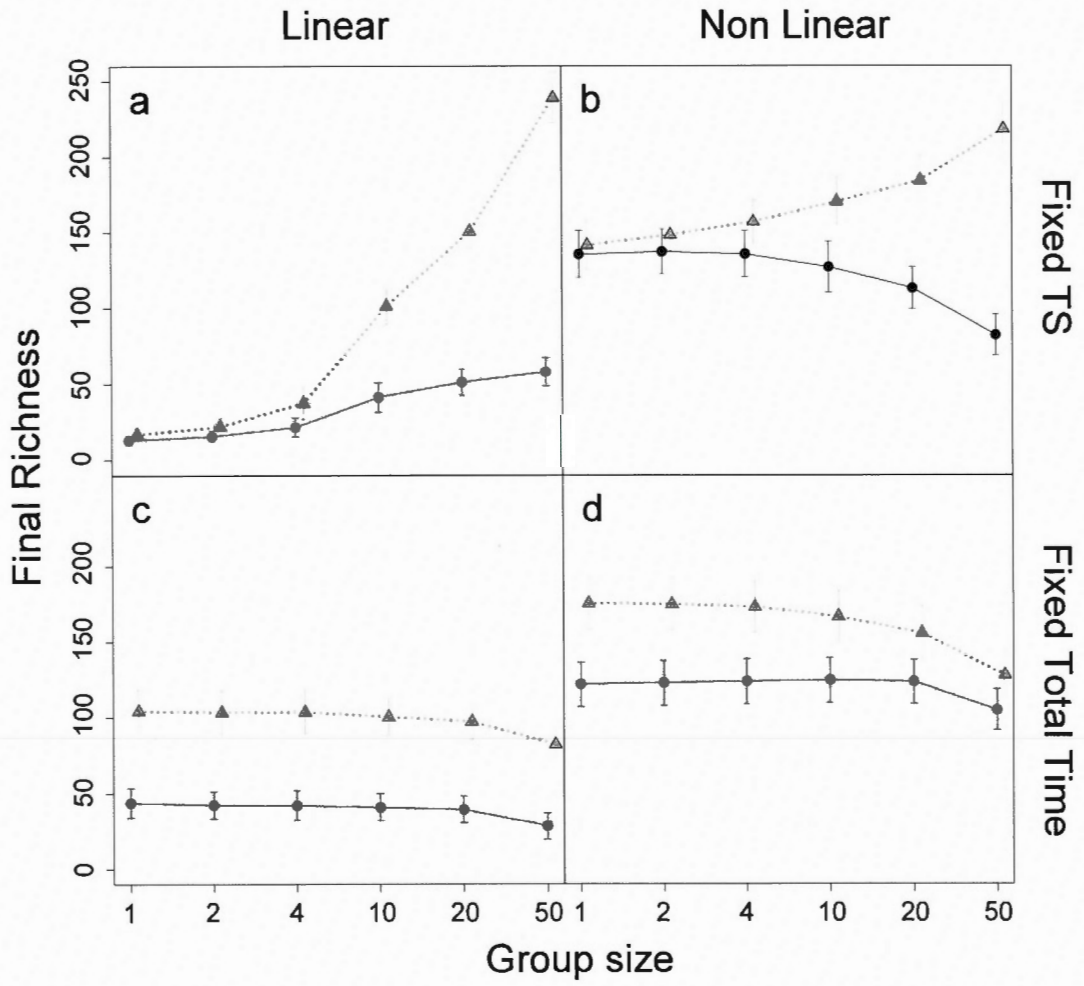

Fig. 5 Effect of aggregation on species richness

Aggregation increases with the number of species arriving together during a single assembly step (Group size). We simulate both linear (a, c) and non-linear functional responses (b, d). In the top panels (a, b) the assembly proceeds according to a fixed timestep: $TS = 20$. In the bottom panels (c, d) the assembly proceeds according to a fixed $total\ time$ equal to 4800. The number of species in a sequence within a simulation is 2400. Points are means over 200 simulations. Grey triangles indicate transient food webs and black circles indicate equilibrium.

4.8.4 Assembly rate ~ Body mass, trophic structure and biomass

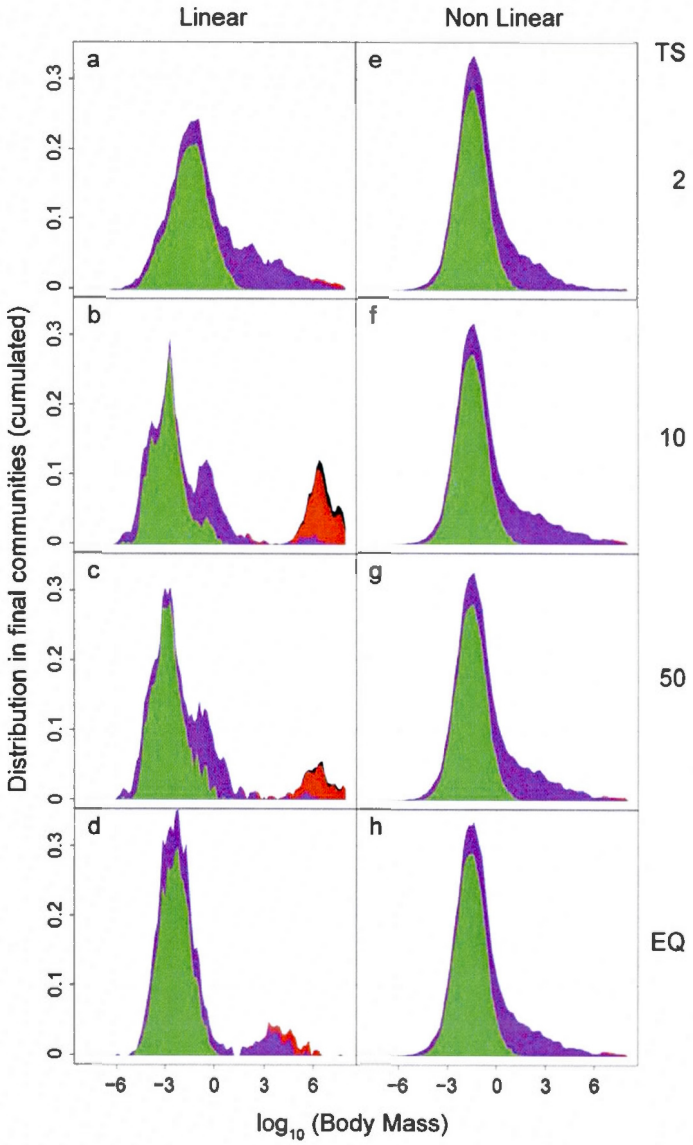

Fig. 6 Effect of assembly rate on the frequency distribution of body mass
We simulate both linear (left panels) and non-linear functional responses (right panels). "EQ" means that the equilibrium is reached at each assembly step. Colors show the trophic levels within cumulated distributions (areas are not overlapping, sum of colored areas equals 1): green areas represent the primary producers; purple areas represent the herbivores and omnivores (species eating only/also plants); red areas represent strict carnivores and black areas represents the transient species, which have no resources but persist thanks to very slow dynamics. Simulations are those of Experiment 1.

Body mass distributions and trophic levels are impacted by the assembly rate and by the type of functional response (figure 6). The food web is highly structured by body mass (several peaks) and changes deeply with assembly rate with linear function response, whereas with non-linear functional responses the body mass distribution is unimodal and does not vary with assembly rate. With linear functional response, the most complex trophic structure is obtained for intermediate TS. Primary producer distribution is skewed toward smaller body masses (fig. B1 for absolute values). Large carnivores are present and we notice gaps in the body mass distribution. When the pace of assembly is very fast ($TS = 2$), very few carnivores persist (fig. A1 for absolute values) and body masses follow a unimodal distribution. When assembly is very slow ($TS = EQ$), producers and consumers have smaller body masses at the end of the assembly process. Species richness decreases (figs 3a and A1), and the food web becomes dominated by producers. In contrast, there are no gaps in the body size distribution with non-linear functional response. Body mass distribution is unimodal, with only very few carnivores (fig. 6, right column), which make the web more connected than with linear dynamics (Appendix, fig. E). The distribution of body masses is insensitive to assembly rate (fig. 6, right column).

Assembly timing also affects the contribution of species to ecosystem biomass (fig. 7), and eventually the total biomass produced in the ecosystem (appendix, figs. A3 and A4 for absolute values). With linear functional responses, we observe a strong diminution of producer contribution to total biomass for intermediate TS (fig.7b and 7c). The contribution of large consumers to total biomass consequently increases compared to the case of rapid assembly. With non-linear functional responses, the total biomass and biomass distribution is relatively insensitive to assembly rate. However, figure 7 shows a gradual shift towards greater contribution of large species to ecosystem biomass with slower assembly rates (fig.7g and 7h, appendix fig. A4), which corresponds to a slight decrease in species average body mass (appendix, fig. B2), and a slight increase in total biomass (Appendix, fig. A4).

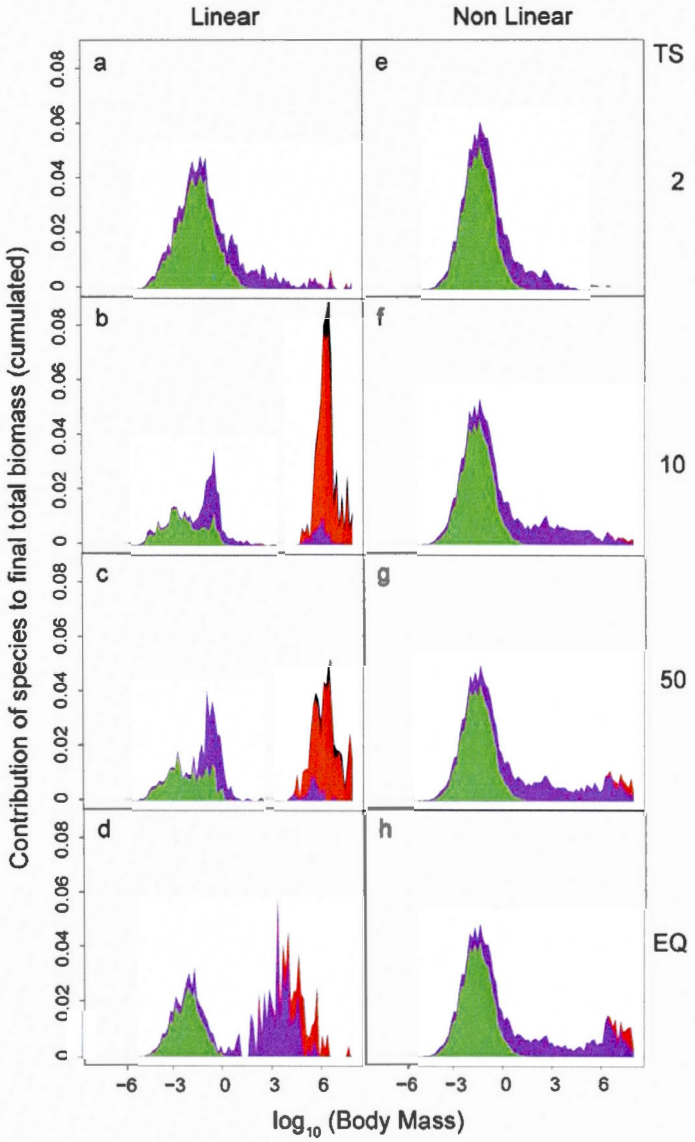

Fig. 7 Effect of assembly rate on the distribution of biomass at equilibrium
Relative contributions of species to ecosystem biomass are plotted against the $\log_{10}$ of their body mass, for food webs at equilibrium assembled with different timesteps *TS* (in lines), and using both linear (left panels) and non-linear functional responses (right panels). "EQ" means that the equilibrium is reached at each assembly step. Colors show the trophic levels within cumulated distributions (areas are not overlapping, sum of colored areas equals 1): green areas represent the primary producers; purple areas represent the herbivores and omnivores (species eating only/also plants); red areas represent strict carnivores and black areas represents the transient species, which have no resources but persist thanks to very slow dynamics. Simulations are those of Experiment 1.

4.9 DISCUSSION

We find that timing-induced variations in community composition and structure are likely to occur according to assembly rate or aggregation with linear functional responses, while food webs where species have non-linear functional responses are much sensitive to aggregation. The variation in assembly rate induces structural changes of food webs, whose magnitudes depend strongly on the functional response. Species persisting only in transient dynamics increase food web richness in sequential assemblies, as well as in simultaneous ones. We discuss these three points, and propose future directions of research.

4.9.1 Timing-induced historical effects for food webs at equilibrium

Differences in the assembly rate produce radically different communities with the same sequence of species introductions for simulations with a linear functional response. Faster rates results in richer food webs. Richness is unchanged by the variability of the interval between introductions because positive and negative effects on richness compensate each other. Divergent assembly trajectories are possible for some particular sequences, in a direction we cannot predict. By contrast with non-linear functional responses, food web richness is unaffected by assembly rate. As a consequence, the variability of the interval between introductions does not affect richness.

The effect of aggregation is understood by the comparison of large group sizes (20, 50) with simultaneous assembly ($TS = 0$). In simultaneous assembly, most consumers are excluded due to small initial densities of their prey. This leads to producer-rich communities with linear functional responses, due to a slow down of the dynamics (we discuss fully this point below in the 'transient' section), whereas with non-linear functional responses, diversity drops to approximately the number of basal resources. Consequently, an increase of the number of simultaneous colonizers may impact positively or negatively final richness of the food web, with either linear or non-linear functional responses respectively (figs. 5a and 5b). However, if the total length of the assembly process is held constant, the opposite effects of aggregation on richness compensate each other, regardless

of the functional response (figs. 5c and 5d). Overall, historical effects may drive the food web to alternative states, even with the same species sequence, if the quantity of colonizers varies for a given total length of the assembly process. Further analyses are needed to assess food webs resistance to invasion (stability), but the clear alternative states we find suggest an important role of assembly timing on food web diversity. This implies that the magnitude of a disturbance may influence eventually the final richness in natural succession if it modifies the isolation of the site from its potential colonizers (Mattews and Endress 2010). Previous modeling studies also show that an increase in assembly rate can lead to complex cyclical endpoints (Lockwood *et al.* 1997), and may interact with dispersal within metacommunities (Fukami 2005).

4.9.2 Structural and functioning changes with assembly rate

With linear functional responses, trophic complexity and ecosystem biomass are maximal for intermediate timesteps, where large omnivores and carnivores persist (figs. 6b and 6c). At intermediate rates, the set up of indirect interactions may allow inferior competitors to maintain before their competitive exclusion occurs. The subsequent greater consumer diversity increases the selection pressure towards smaller primary producer operating along the assembly process. This "ecological selection" (*sensu* thesis, chapter 3) occurs because assembly proceeds by successive competition events between residents and colonizers, and apparent competition is won by the species that can sustain the highest consumer biomass (Holt and Lawton 1994, Holt *et al.* 2001, Chase *et al.* 2002, Chesson and Kuang 2008), which are the smallest species (thesis, chapter 3). The smallest bodied producers are more productive (Brown *et al.* 2004), which benefits consumers and enables the establishment of carnivores. Herbivory and predation pressures create gaps in the body mass distribution by body mass displacement of their prey. By contrast, when assembly is too fast, strict carnivores are excluded since preys with small initial densities do not provide them enough food (fig. 6a). Diversity drops when assembly is very slow because competition excludes some species and fewer niches are available for higher trophic levels (fig. 6d, and appendix fig. A1).

The body mass distribution is very different with a non-linear functional response. First, the scarcity of large consumers and strict carnivores may be a consequence of reduced individual biomasses of their potential preys (appendix, see biomass and richness in fig. A, compared to linear functional response). This can also explain the unimodal species body mass distribution: since preys have lower equilibrium biomass with non-linear functional response, they may be able to sustain only consumer populations with not too large body mass relative to them (food requirements are positively related to body mass; thesis chapter 3). Consequently, the body mass distribution in the food web is compressed. This compression of consumer body size distribution leads eventually to a higher food web connectance than with a linear functional response (appendix, fig. E). Higher connectance may contribute to the insensitivity of trophic structure to changes in assembly rate with a non-linear functional response (fig. 6, right column): the consumer richness may change only slightly with assembly rate because high connectance prevents extinction cascades that might follow the potential exclusion of a prey (Dunne *et al.* 2002). However, even if it is not detectable in figure 6, body mass distribution is still slightly sensitive to assembly rate: the largest consumer species, including strict carnivores, contribute more to ecosystem biomass as assembly rate slows down (fig. 7, right column and appendix fig. A4). This is due to an increase of the selection pressure towards smaller and more productive species at the basis of the food web (appendix, fig. B4). The subsequent improvement of productivity benefits the carnivore persistence, which was null at very fast assembly rates. Moreover, the much greater richness of food webs when the functional response is non-linear, compared to linear, denotes that interaction non-linearity adds essential supplementary coexistence mechanisms (Armstrong and McGehee 1980, Chesson 1994, Huisman and Weissing 1999).

4.9.3 Transient versus equilibrium dynamics

Transient persistence was observed without sequential assembly ($TS = 0$), and with linear functional responses, despite our conservative method to detect stationary states. This result stresses important points on the interaction between assembly and local dynamics.

Species are introduced at very low density and therefore for the simultaneous assembly only primary producers can persist (appendix, figs. A1 and C). In this configuration, the competitive exclusion between producers makes species richness decline to the number of resources (Gause 1934, Tilman 1982, Chase and Leibold 2003). We observe this situation with a non-linear functional response. Instead, with a linear functional response, more than eighty producers persist for a transient period thanks to very slow food web dynamics. We identify three possible mechanisms responsible for transient coexistence. First, the simultaneous assembly of many species reaches slowly the stationary state due to complex indirect interactions. Second, the selection pressure is so high that the remaining producers are very similar (see the low variance of producer traits in figs. B1 and B3 for $TS = 0$), and this leads to transient coexistence of quasi-neutral species (Gravel *et al.* 2006, Scheffer and Van Nes 2006). The homogenous initial density across species may also drive the system close to saddle points with a slow down of the dynamics (Cushing *et al.* 1998, Hasting 2004). Food web models usually use random initial densities to prevent the contraction of the food web to producers (Brose *et al.* 2006b, Berlow *et al.* 2009). Third, some consumers with large body mass maintain themselves due to their slow metabolism (Brown *et al.* 2004), and slows down the whole web dynamics. This mechanism also holds for slower assembly rates, since some large species without resource persist over a transient period (fig. 6b and 6c). This third mechanism stresses that differences between species metabolism corresponds to differences in the time needed to reach stationary state. As a consequence, small species may spend most of the time close to equilibrium owing to their fast growth rate, whereas large species may never be at equilibrium. Moreover, trophic links may relate species even indirectly, such that the presence of big species slows down interaction dynamics, and prevent many species to reach equilibrium. This size/scale-dependency of dynamics have been analyzed and reviewed by Hastings (2004), but have not been yet discussed in studies using bioenergetic food web models. Further analyzes should investigate the extent to what such mechanism acts in food web bioenergetic models using non-linear dynamics, and possibly affects the detection of stationary state.

Transient food webs display a greater richness than equilibrium food webs, but this depends on assembly timing (figs. 3 and 5). Weak competitors are able to maintain themselves shortly during the transient dynamics, and richness decreases if colonization events do not recurrently provision it with new species. The implications of our observations for natural systems are not so trivial since disturbances may frequently move ecosystems from their equilibrium (Attiwill 1994, Turner *et al.* 1998, Borics *et al.* 2013). Frequent disturbances may promote coexistence in very different ecosystems, as proposed by the "Intermediate Disturbance Hypothesis" (*sensu* Connell 1978, Knowlton 2004, Molino and Sabatier 2001). In such case where disturbance regime maintains diversity, it may be relevant to focus on alternative transient states rather alternative stable states (Fukami and Nakajima 2011, 2013). Our results show that transient coexistence can lead to qualitatively different effects of assembly rate on species richness. Presumably, if disturbances are repeated, then after the assembly rate is susceptible to impact long term coexistence. Interestingly, simulations with linear and non-linear responses display the same response to assembly rate, with species richness increasing with faster rates (fig. 3a). Bastolla and colleagues (2001) also found a positive relationship between transient coexistence and the number of species arriving by unit of time, for various models without energetic constraints. Our approach was designed to isolate the effects of assembly timing from species sequence. We chose to focus first on equilibrium food webs because we wanted to investigate mechanisms other than immigration. However, we believe that interesting insights on the dependence of food web structure and functioning on assembly features may emerge from analyses of transient dynamics.

4.9.4 Conclusion

Our results show that the characteristics of food web assembly dynamics may impact richness, structure and functioning, independently from the sequence of species introductions. This suggests that the development and recovery of ecosystems may vary according to disturbance features through their influence on assembly timing (Paine *et al.* 1998). Our bioenergetic approach enables to bridge succession and community assembly

theory by linking processes of ecosystem development (biomass production) to species traits and food web structure.

4.10 ACKNOWLEDGEMENTS

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4.11 APPENDIX – SUPPLEMENTARY FIGURES

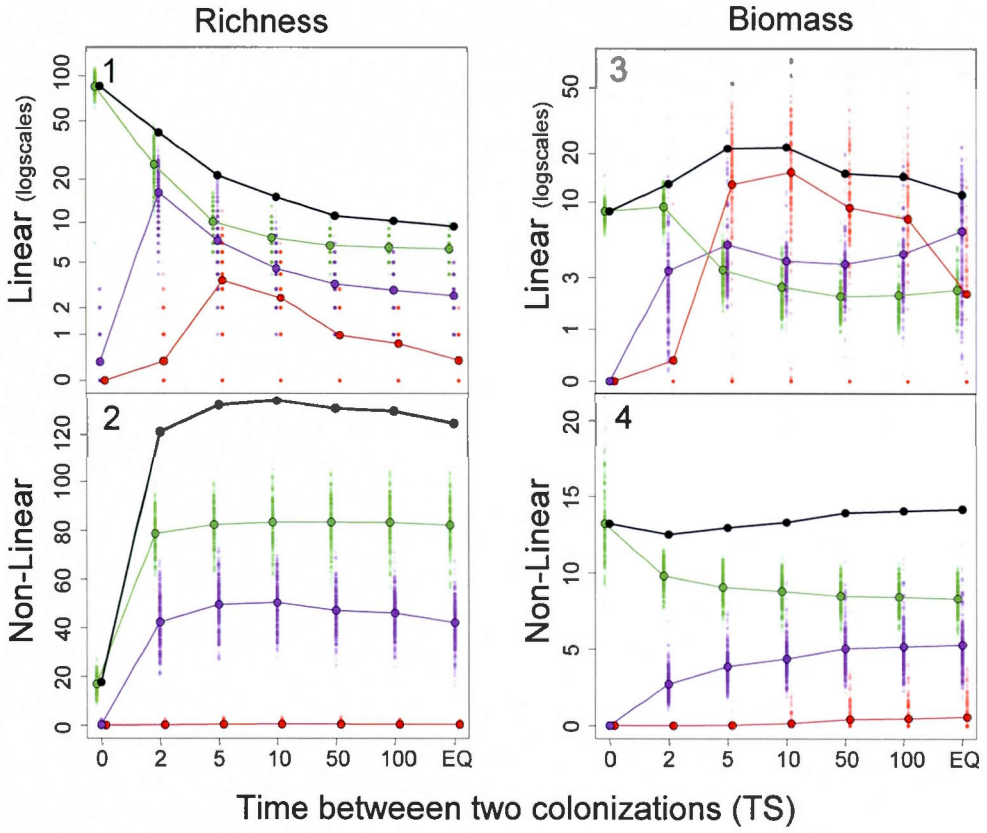

Fig. A Final food web richness and biomass in experiment 1

The richness (left panels) and summed biomass (right panels) in final equilibrium food webs, assembled using either linear (top panels), or non-linear functional responses (bottom panels) are plotted against the timestep TS (time between 2 colonization events). "EQ" means that the equilibrium is reached at each assembly step. Small points represent simulations and larger circled points are means over 200 simulations. Green, purple, red and black color refer respectively to primary producers, species eating plants (herbivores and omnivores), strict carnivores and sums overs all species.

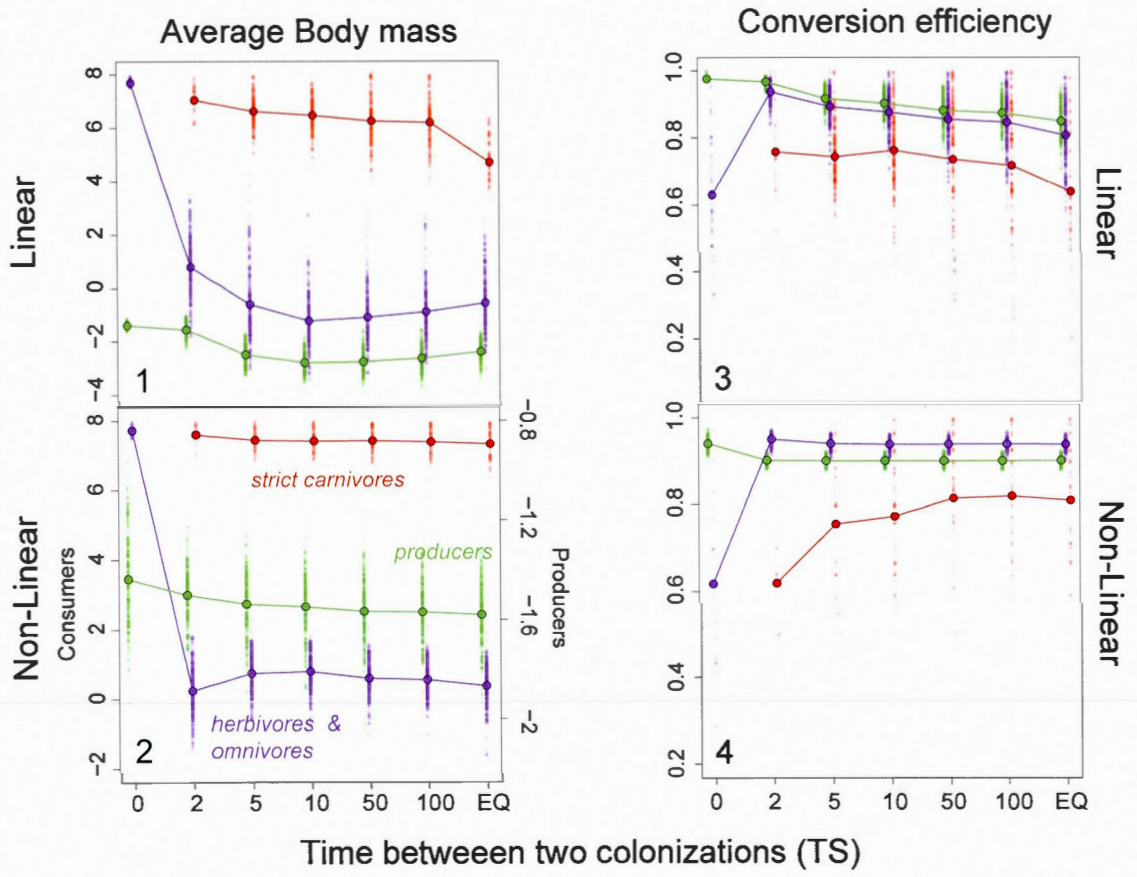

Fig. B Average species traits in final food webs of experiment 1

The average body mass (left panels) and conversion efficiency (right panels) of species in final equilibrium food webs, assembled using either linear (top panels), or non-linear functional responses (bottom panels) are plotted against the timestep TS (time between 2 colonization events). "EQ" means that the equilibrium is reached at each assembly step. Small points represent simulations and larger circled points are means over 200 simulations. Green, purple, red and black color refer respectively to primary producers, species eating plants (herbivores and omnivores), strict carnivores and sums overs all species.

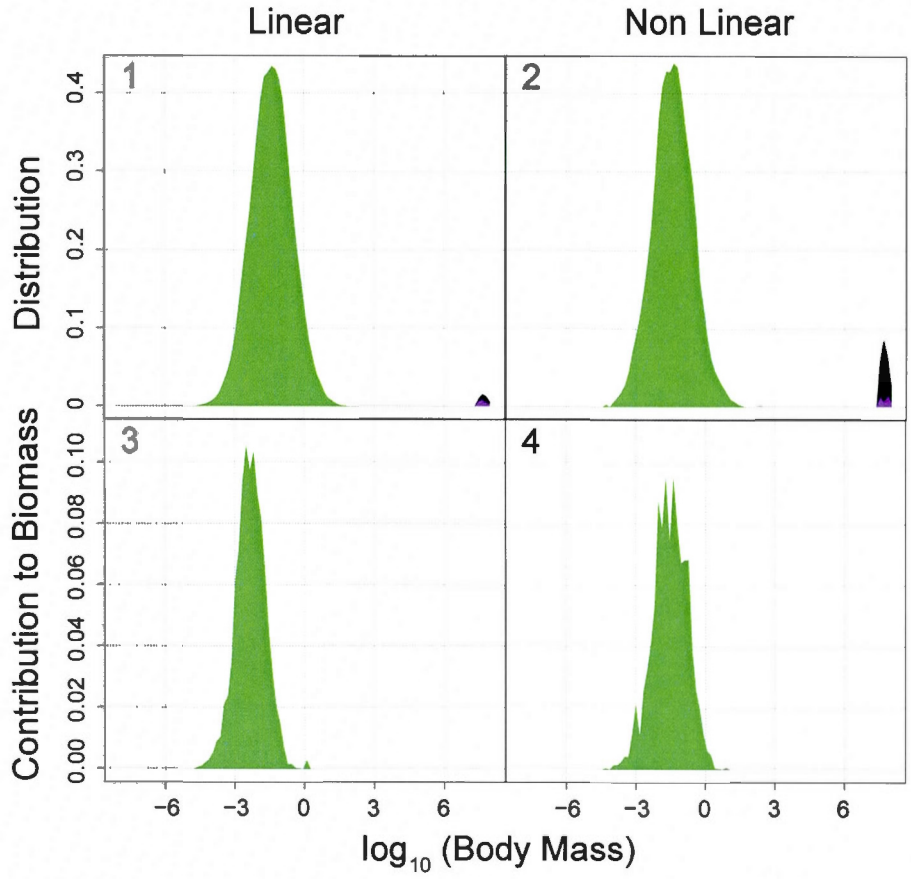

Fig. C Body mass and contribution to biomass of species in food webs resulting from simultaneous assembly ($TS = 0$)

Top panels show the density distribution of the $\log_{10}$ of species body mass within food webs at equilibrium. Bottom panels show the relative contributions of species to ecosystem biomass according against $\log_{10}$ of their body mass. In the left panels species have linear functional responses, whereas in the right panels they have non-linear functional responses. Colors show the trophic levels within cumulated distributions (areas are not overlapping, sum of colored areas equals 1): green areas represent the primary producers; purple areas represent the herbivores and omnivores (species eating only/also plants); black areas represents the transient species, which have no resources but persist thanks to very slow dynamics.

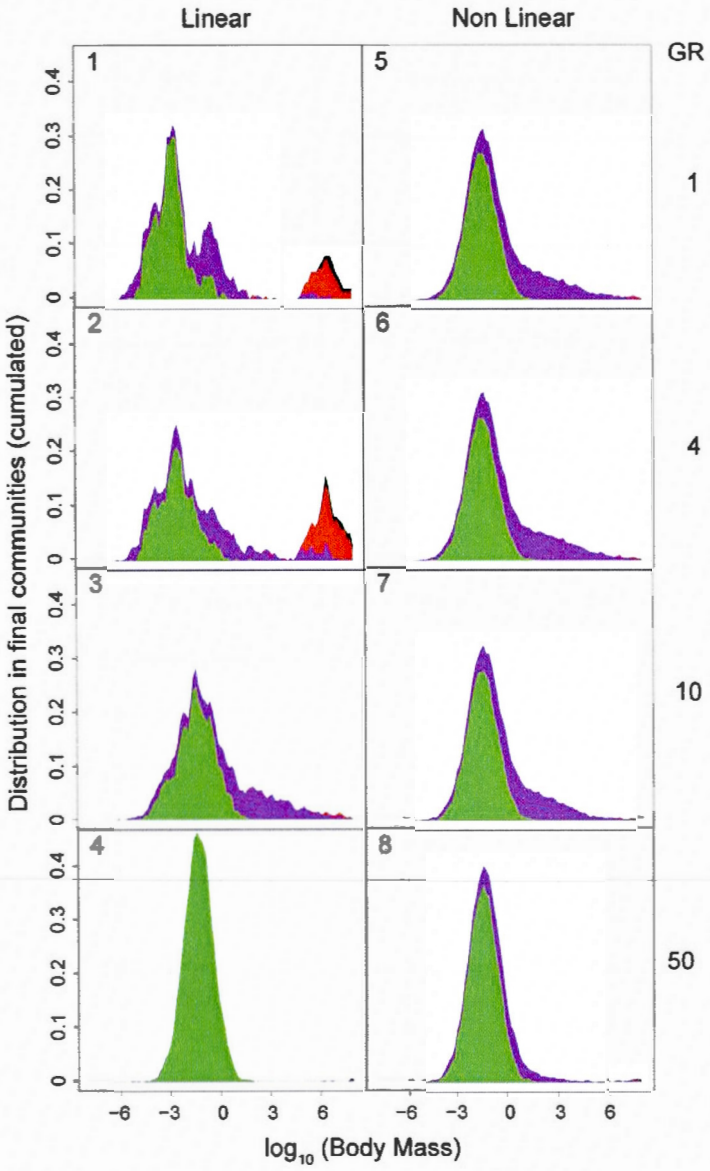

Fig. D Contribution of species to biomass according to their $\log_{10}$ (body mass) in final food webs (Experiment 3, fixed $TS = 0$)

The relative contributions of species to ecosystem biomass are plotted against the $\log_{10}$ of their body mass, for final food webs at equilibrium assembled with different group sizes (number of species colonizing the ecosystem in a single assembly step) *GR* (in lines), and using either linear (left panels), or non-linear functional responses (right panels). Colors show the trophic levels within cumulated distributions (areas are not overlapping, sum of colored areas equals 1): green areas represent the primary producers; purple areas represent the herbivores and omnivores (species eating only/also plants); red areas represent strict carnivores and black areas represents the transient species, which have no resources but persist thanks to very slow dynamics

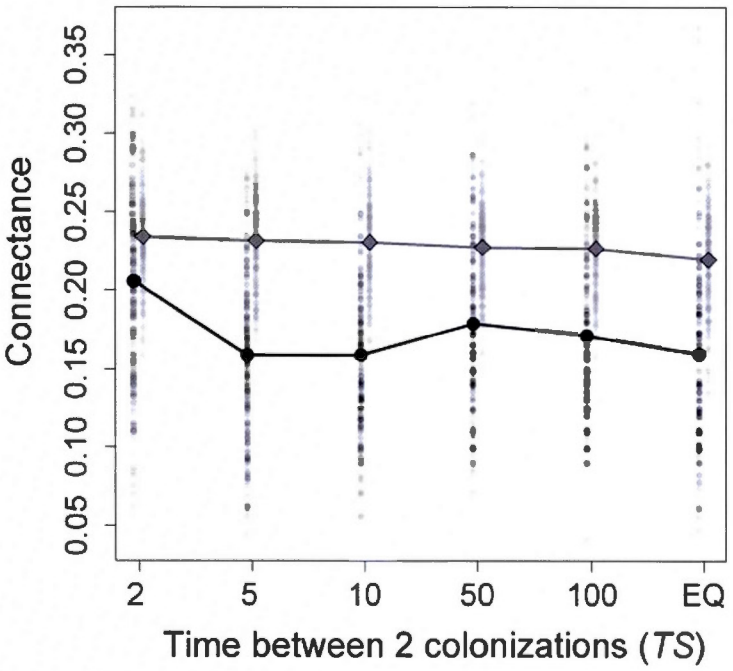

Fig. E Connectance of final food webs (Experiment 1)
The connectance in final equilibrium food webs, assembled using either linear (black circles), or non-linear functional responses (grey diamonds) is plotted against the timestep TS (time between 2 colonization events). "EQ" means that the equilibrium is reached at each assembly step. Small points represent simulations and larger points are means over 200 simulations.

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CHAPITRE 5
ASSEMBLAGE DES ÉCOSYSTEMES (3) : RECYCLAGE ET BOUCLE D'INTERACTION ENTRE BIODIVERSITE ET FONCTIONNEMENT DES ECOSYSTEMES

5.1 TITRE

Quand la diversité favorise-t-elle la diversité ? Une boucle de rétroaction entre diversité et fonctionnement des écosystèmes

5.2 RÉSUMÉ

L'écologie des écosystèmes et l'écologie des communautés se sont longtemps opposés sur la relation entre biodiversité et fonctionnement des écosystèmes (BEF). La première affirmait que la diversité varie avec la productivité selon une relation *en cloche*, tandis que la seconde affirmait que la productivité variait selon une relation positive avec la diversité. Finalement ces apparentes contradictions ont été réconciliées dans une perspective multi-échelles, qui a beaucoup aidé à comprendre les observations empiriques. Cependant, une intégration mécaniste de ces vues manque toujours.

Ici nous proposons le recyclage comme étant le processus permettant de compléter la boucle de rétroaction entre diversité et fonctionnement des écosystèmes. Nous développons un modèle Bioénergétique d'Assemblage d'Ecosystème (BEA model) où diversité spécifique, productivité et fertilité environnementale interagissent explicitement durant le développement de l'écosystème, par le biais du couplage entre un réseau trophique « autotrophe » (basé sur les nutriments inorganiques) et un réseau trophique détritivore. Nous utilisons ce modèle pour caractériser comment le recyclage affecte la diversité et fonctionnement des écosystèmes au cours de la dynamique d'assemblage, et par là la relation BEF.

Nous trouvons que le recyclage facilite l'installation d'espèces uniquement pour des valeurs intermédiaires de fertilité environnementale. Pour ces valeurs, diversité et productivité augmentent avec le recyclage et la force de leur relation dépend de l'efficacité du recyclage. Plus globalement, l'influence de l'efficacité du recyclage sur la relation BEF dépend de la fertilité environnementale et des métriques utilisées pour caractériser le fonctionnement de l'écosystème (production versus productivité). L'exploration du modèle BEA a permis de poser des bases théoriques pour compléter le cadre conceptuel d'explication de la relation BEF pour les réseaux trophiques complexes, et de créer un pont mécanistique entre la dynamique d'assemblage des communautés et le développement des écosystèmes.

Cet article intitulé « When does diversity enhance diversity? A feedback loop between diversity and ecosystem functioning » a été co-rédigé par mes directeurs de thèse Dominique Gravel et Nicolas Mouquet, la chercheuse Sonia Kéfi et moi-même. Le manuscrit est en préparation pour être soumis pour publication dans la revue *Ecology Letters*. Dans cette optique, la discussion a encore besoin d'être approfondie et complétée, notamment en comparant des résultats avec ceux obtenus par les modèles dynamiques plus simples évoqués en introduction, et en les replaçant par rapport aux études empiriques.

En tant que première auteure, j'ai fait la recherche bibliographique, participé à l'élaboration du modèle, duquel j'ai réalisé la programmation. J'ai aussi analysé les résultats, produit les figures et ainsi que réalisé l'essentiel de la rédaction. Dominique Gravel, dernier auteur, et Nicolas Mouquet, 2nd auteur, ont proposé l'idée originale et la structure du modèle. Dominique Gravel et Sonia Kéfi, 3ème auteure, ont participé aux choix plus techniques et à la résolution des problèmes mathématiques et numériques. Philippe Desjardins-Proulx, 4ème auteur, a fournit une assistance technique à la programmation. Nicolas Mouquet, Sonia Kéfi et Dominique Gravel ont participé à la rédaction et à l'interprétation des résultats.

5.3 TITLE

When does diversity enhance diversity? A feedback loop between diversity and ecosystem functioning

5.4 ABSTRACT

Ecosystem and community ecology have long had opposed views on the relationship between Biodiversity and Ecosystem Functioning (BEF). The former argued that diversity varies with productivity according to a hump-shaped relationship, whereas the later argued that productivity varies positively with diversity. This apparent contradiction has since then been reconciled in a scale-dependent perspective, which greatly helped understanding empirical observations. A mechanistic bridge between these views is nonetheless lacking. Here, we propose nutrient cycling as the missing process closing the loop between biodiversity and ecosystem functioning. We develop a Bioenergetic Ecosystem Assembly model (BEA model) where species richness, productivity and ecosystem fertility affect each other during the ecosystem development, through interactions between an autotroph and a detritivore food web. We characterize how recycling affects diversity and ecosystem functioning during the assembly process and thereby the BEF relationship. We find that recycling facilitates species establishment only for intermediate fertility. In such conditions, diversity and species productivity increase with recycling, and the strength of the BEF relationship depends on recycling efficiency. Overall, the influence of recycling on BEF relationship varies with ecosystem fertility and the metric used for ecosystem functioning. Our analysis of the BEA model completes the BEF framework for complex food webs and couples community assembly dynamics and ecosystem development through biomass recycling.

5.5 KEYWORDS

BEF relationship, recycling, facilitation, ecosystem assembly, aboveground-belowground linkages, succession

5.6 INTRODUCTION

The interplay between biodiversity and ecosystem functioning is a central research theme linking community and ecosystem ecology (Chapin *et al.* 2000, Loreau *et al.* 2001, Hooper *et al.* 2005, Duffy *et al.* 2007) and stability (Loreau and De Mazancourt 2013). A number of studies have explored different facets of the biodiversity-ecosystem functioning (BEF) relationship (Loreau *et al.* 2001; Hooper *et al.* 2005). However a comprehensive mechanistic integration of the feedbacks between diversity and ecosystem functioning is lacking. Here, we propose to include the reciprocal interaction between diversity and ecosystem functioning explicitly through the recycling of nutrients contained in the organic matter. We investigate this loop in the context of food web assembly and ecosystem development to identify its effects on the BEF relationship.

The numerous studies on BEF relationship have first lead to apparently contradicting results in the late 90's (Grime 1997, Huston 1997, Schmid 2002). Ecosystem ecologists, focusing on flows of energy and matter in ecosystems through primary production, found a hump-shaped BEF relationship *(Fig. 1 middle arrow*; Huston and DeAngelis *1994,* Waide *et al.* 1999, Grime 2001). They measured the diversity of sites along gradients of productivity and found that diversity was higher in sites with intermediate productivity, owing to a more favorable balance between resource availability and competition (Bobbink *et al.* 1998, Leibold 1999, Dodson *et al.* 2000, Mittelbach *et al.* 2001). In contrast, community ecologists, focusing on the interactions between species, manipulated plant species richness and found a positive relationship between diversity and productivity (Fig. 1, bottom left arrow; Hector *et al.* 1999, Tilman *et al.* 1997a, 2001). It is commonly accepted that a more diverse set of species has a higher probability of containing a highly productive species ('sampling' or 'positive selection effects': Tilman *et al.* 1997b, Loreau

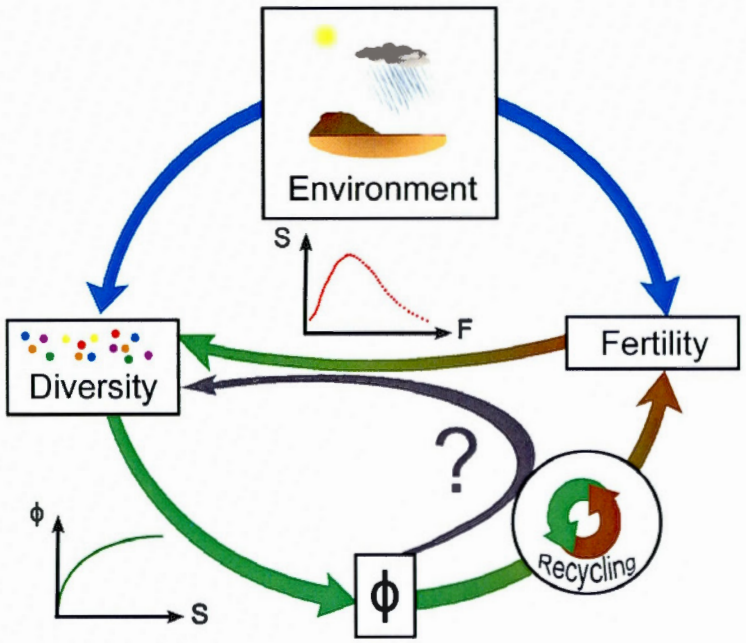

Fig. 1 The BEF feedback loop

Figure 1 shows our conceptual framework integrating recycling into the Biodiversity-Ecosystem functioning relationship. The environment determines the local fertility and limits diversity by filtering species traits. Local fertility *F* enhances local diversity *S* for intermediates levels (ecosystem ecology view), which diversity in turn maximizes the realized productivity ϕ (community ecology). Productivity influences in turn fertility via recycling. Then we expect a feedback loop of diversity on itself (grey arrow).

1998a) and of enhancing resource use by niche complementarity or facilitation ('complementarity effect': Loreau 1998a and b, Gross and Cardinale 2005, Gross *et al.* 2007, Cardinale *et al.* 2007). Both mechanisms contribute to increase productivity when diversity is higher (Loreau et al. 2001, Friedley 2002, Fargione *et al.* 2007).

The proposition of a conceptual multi-scale framework and clarifications of the measures of ecosystem functioning reconciled these apparently contrasting views of the BEF relationship (Loreau *et al.* 2001, Schmid 2002, Hooper *et al.* 2005, Loreau 2010a). The "ecosystem" approach illustrates how the *potential productivity* of different sites

influences the realized diversity (Grime 2001), whereas the "community" approach illustrates how diversity influences the *realized productivity*. The potential productivity is quantified by fertility (the amount of resource available for building up the biomass), and the realized productivity by either the standing biomass (Tilman *et al.* 1997a), its turnover (hereafter called *productivity*), or its production (Hector *et al.* 1999). Environmental factors determine local fertility (e.g. nitrogen deposition, soil properties, watershed configurations, Elser *et al.* 2009) and limit diversity by filtering species traits (Cottenie 2005, Van der Gutsh *et al.* 2007; Fig. 1, top arrows). Finally, a last feedback arrow lacks in our verbal scheme of the relationship between diversity and ecosystem functioning (Fig. 1, grey arrow) since realized productivity is also expected to influence in turn fertility via recycling (Tiessen *et al.* 1994). This last feedback has not yet been considered explicitly in the BEF debate and will constitute the core of our study.

Autotroph species synthesize organic matter from inorganic nutrients and energy (e.g. solar), supplying food at the basis of ecological communities. Biomass of living organisms is progressively transformed into detritus through their catabolism (Moore *et al.* 2004). Detritus serve as basal resources for detritivores (Moore *et al.* 2004). Moreover consumer – resource interactions are far from being totally efficient in converting food into new biomass (Hairston and Hairston 1993). Species lose or excrete nutrients, which return into the cycle as resources for autotrophs (Jones 1998, McIntyre *et al.* 2007). Hence, organic matter is recycled into inorganic nutrients via a direct pathway (*e.g.* fish excretion: Vanni 2002), or indirectly via the decomposition and mineralization of detritus by the detritivore web (Clarholm 1985, Scheu 2002, Moore *et al.* 2004).

Although in some specific environments recycling may be marginal (e.g. frozen soils, ocean bottom: Coûteaux *et al.* 1995, Raven and Falkowski 1999), ecologists have stressed recycling as a key process of many ecosystems' functioning (Tiessen *et al.* 1994). Recycling contributes to the formation of soils during the primary succession (Margalef 1963, Odum 1969). In tropical forests standing on poor and leached soils, rapid nutrient cycling is critical to retain phosphorus within the ecosystem (Vitousek and Sanford 1986, Tiessen *et al.* 1994, Attiwill and Adams 1995). There is a substantial amount of knowledge

on the effects of plants on the recycling process (Prescott 2002, Bartelt-Ryser *et al.* 2005, Hättenschwiler *et al.* 2005, Meier and Bowman 2008, Cornwell *et al.* 2008) and on the feedback of microbial communities and detritivores on plant diversity (Facelli and Pickett 1991, Bever *et al.* 1997, Wardle 2006, Wardle *et al.* 2004, Moore *et al.* 2004, Van der Heidjen *et al.* 2008). The microbial community played also a crucial role on the provision of nutrients for phytoplankton production (Tranvik 1992), as well as fish and aquatic mammals excretion (Urabe *et al.* 2002, Vanni 2002, Roman and McCarthy 2010). These different examples show the fundamental role of recycling in supplying a substantial part of basal resources to many food webs.

However, the recycling process has yet to be fully integrated into food web models. DeAngelis (1980, 1992) identified the positive role of nutrient cycling on ecosystem resilience with the study of linear food chains. Further models have explored more complex interactions with recycling. They for instance investigated competition between plants (Loreau 1998a), interaction between different recycling pathways (De Mazancourt *et al.* 1998), competition between and within plants and decomposers (Loreau 1998b) and with the addition consumers (Loreau 2001) when recycling is integrated. These studies provided bases for a mechanistic understanding of BEF relationship for relatively simple foodwebs, pointing also the variation of BEF relationship with the diversity and specialization of species within trophic levels (Thébault and Loreau 2003, 2005, 2006). Nonetheless, the specific role of feedbacks mediated by recycling on the BEF relationship in complex food webs remains an open question.

A comprehensive analysis of the feedback between biodiversity and ecosystem nutrient cycling should account for the dynamic process of ecosystem development (Margalef 1963, Odum 1969). Ecosystems are rarely at equilibrium because of disturbances and environmental fluctuations (Pickett *et al.* 1989). During the early phase of community assembly, increasing diversity will enhance the production of biomass (Fig. 1, community ecology). This increase in biomass production should enhance fertility via recycling and then feed back on the realized diversity (ecosystem ecology) by facilitating the colonization of new species. Therefore an emergent facilitation should occur through recycling, inducing

a positive feedback of diversity on itself. Eventually competition for resources will come into play, limiting coexistence, and ecosystem functioning will stabilize at a level determined by ecosystem intrinsic fertility.

Our objective in this study is to investigate the feedback loop between diversity and ecosystem functioning through recycling. We develop a Bioenergetic Ecosystem Assembly model (BEA model) where recycling is explicitly represented by the coupling between autotroph and detritivore food webs. This allows species richness productivity and ecosystem fertility to feed back explicitly on each other during ecosystem development. We analyze how recycling affects invasibility, food web structure and ecosystem functioning through assembly dynamics. We intend to characterize in the end how the recycling affects the BEF relationship. We adopt a comparative approach contrasting simulations of ecosystem assembly where recycling is included or not. We structure our study with 3 interrelated questions:

(1) Do we observe a facilitation effect of recycling on species colonization success?

(2) What does recycling efficiency affect food web and ecosystem functioning along the assembly process?

(3) How do recycling and ecosystem fertility interact and shape the BEF relationship?

5.7 METHODS

5.7.1 Model description

The BEA model is a bioenergetic ecosystem model coupling two food webs with a recycling loop (autotroph and detritivore webs, see Fig. 2). The model describes the fluxes of nutrients among compartments, and we assume biomass to be directly proportional to nutrient content. The dynamics of the 4 different types of compartments (inorganic resources R, producers P, consumers C or detritus D) is described by the following set of ordinary differential equations [1]:

$$\frac{dR_i}{dt} = I + \rho\left[\sum_j \sum_k \left(\frac{1}{\varepsilon_j} - 1\right) Y_j \omega_j B_j B_k\right] \Big/ nress - \sum_{j \in P_{auto.}} Y_j \omega_j B_j R_i - e_i R_i$$

$$\frac{dP_i}{dt} = \sum_{j \in \{R,D\}} Y_i \omega_i B_j P_i - X_i P_i - \sum_{j \in C} Y_j \omega_j B_j P_i - e_i P_i$$

$$\frac{dC_i}{dt} = \sum_{j \in \{P,C\}} Y_i \omega_i B_j C_i - X_i C_i - \sum_{j \in C} Y_j \omega_j B_j C_i - e_i C_i$$

$$\frac{dD_i}{dt} = \sum_{j \in \{P,C\}} X_j B_j \Big/ ndet - \sum_{j \in P_{det.}} Y_j \omega_j B_j D_i - e_i D_i$$

We first present the flows of nutrients in the ecosystem and then detail the trophic interactions. Inorganic resources, R_i, representing different niches for primary producers (e.g. nutrients at different depths in a soil or inorganic forms; Moore *et al.* 2004), are continuously supplied by an external input I (e.g. deposition, alteration). Primary producers ($P_{auto.}$) feed on these inorganic resources and support consumers of the autotroph-based web (green P_i and C_i compartments in Fig. 2). Producers and consumers excrete faeces and die proportionally to their metabolic rate X_i, which uniformly supply different classes of detritus, D_i. These detritus in turn support a second web of the same structure with secondary producers ($P_{det.}$) and consumers (brown P_i and C_i compartments in Fig. 2). Symbols $nress$ and $ndet$ refer to the number of classes of either nutrients or detritus. Because consumption by species is not completely efficient, a part $1/\varepsilon_i - 1$ of each uptake is lost (*e.g.* canopy leaching, excretion), where ε_i is the assimilation efficiency (Brose *et al.* 2006b). We attribute a lower efficiency to species of the detritivore web than to those of the autotroph-based web, assuming that they contribute more to recycling through mineralization (see Table 1 for parameter values). A part ρ (efficiency of recycling) returns directly into inorganic form via recycling and supplies uniformly the different classes of inorganic nutrients, hence closing the recycling loop. The other part $(1 - \rho)$ is leached out of the system. The ecosystem also loses nutrients from each compartment at a constant rate e_i (*e.g.* leaching, sedimentation; Asper *et al.* 1992).

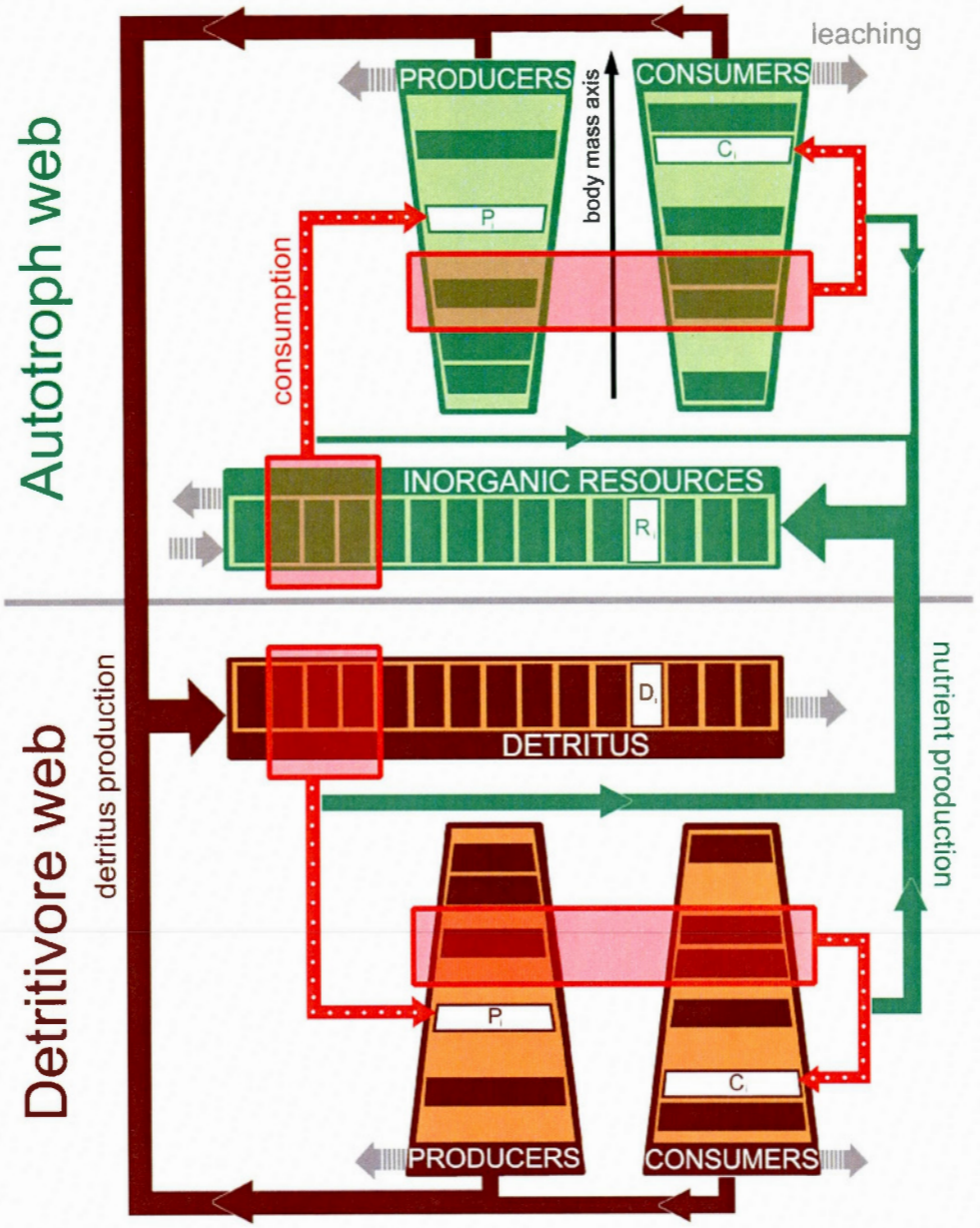

Fig. 2 Model structure

The model links an autotroph-based food web (top green compartments) to a detritivore food web (bottom brown compartments) via the recycling process. Autotroph producers feed on different classes of inorganic resources and are consumed by consumer species according to their body mass. Species produce detritus (brown arrows), which supply uniformly different classes of detritus. Detritus are the basal resource for the detritivore web, based on the same structure than the autotroph-base web. Consumption by species (red arrows) is not totally efficient. A part of nutrient uptake supplies directly and uniformly the classes of inorganic resources. Inorganic resources are also supplied by external inputs and nutrients are leached out from the ecosystem by all compartments (grey arrows).

Table 1: Symbols and values of the parameters used for the simulations

Symbols	Description	Dimensions	Values
R_i, P_j, C_k, D_l	Densities* of Inorganic Resource i, Producer j, Consumer k, Detritus l, respectively. P and C refer to producers or consumers of both webs.	$M.L^{-2}$	–
I	Input of inorganic nutrient	$M.L^{-2}.T^{-1}$	$\{0.02, 0.03, 0.05, 0.1, 0.5, 1, 5\ 20\}$
e_i	Output rate of species or resource i	T^{-1}	0.1
$nress, ndet$	Numbers of inorganic resources and detritus	$dimensionless$	10
F	Environmental fertility	$M.L^{-2}$	$F = (I/e_i) \times nress$
ρ	Recycling efficiency (RE): proportion of the nutrient production that is recycled	$dimensionless$	$\{0, 0.5, 0.9, 1\}$
M_i	Specific body mass of species i *(C: data from Brose et al. 2005)*	M	C: $logN(-1.67, 6.25)$ P: $logN(-2.50, 6.25)$
ε_i	Conversion efficiency of species i Normal distributions for P and C of autotroph-based and detritivore webs in this order.	$dimensionless$	$P_{auto}: N(0.85, 0.20)$ $C_{auto}: N(0.70, 0.20)$ $P_{det}: N(0.60, 0.20)$ $P_{det}: N(0.70, 0.20)$
a_x	Allometric constant for the metabolic rate. Values for producers, invertebrates and vertebrate ectotherms, respectively	$T^{-1}.M^{1/4}$	$\{0.138, 0.314, 0.880\}$ (Brose *et al.* 2006b)
a_y	Allometric constant for the maximum consumption rate. Values for producers, invertebrates and vertebrate ectotherms, respectively	$T^{-1}.M^{1/4}.(M.L^{-2})^{-1}$	$\{1, 2.512, 3.520\}$ (Brose *et al.* 2006b)
X_i	Metabolic rate of species i	T^{-1}	$a_x M_i^{-0.25}$
Y_i	Maximum consumption rate of species i	$T^{-1}.(M.L^{-2})^{-1}$	$a_y M_i^{-0.25}$
ω_i	Preference of species i for each of its n resources	$dimensionless$	$1/n$

* *Note that density means stock or biomass by unit of surface, not abundance of individuals.*

The niche and the demographic parameters are based on average specific body mass M, like in the bioenergetic models developed after Yodzis and Innes 1992's model (Brose *et al.* 2005, 2006b, Brose 2008, Berlow *et al.* 2009). We assign a body mass M to each species, randomly drawn from a lognormal distribution fitted on empirical data (from Brose *et al.* 2005). Producers are allowed, at random, to consume 1 to 3 consecutive basal resources (either inorganic resource or detritus depending on which web they belong to).

Consumers feed on either producers or consumers within their affiliation web according to the niche model (Williams and Martinez 2000). For simplicity, we do not consider consumers that would feed in both autotroph and detritivore webs, even if it may be common in nature (Scheu 2001). The position of all species on the niche axis is given by the log10 of their body mass. The diet optimum of a consumer of a given body mass is provided by an empirical, linear positive relationship between prey and predator body masses (Brose et al. 2006a). The boundaries of the diet are given by the 10% and 90% quantile regressions (Gravel *et al.* 2013). Consumers prey on all species whose body mass fall into the diet range. We assume producers to have a lower body mass than consumers on average (see Table 1 for values of their lognormal distribution). We use linear functional responses to keep the dynamics simple in this first study using the BEA model, even if we recognize it might limit coexistence (Chesson 2000). Species i gains biomass from the consumption on species j's biomass B_j according to its maximum consumption rate Y_i and a preference term ω_i. The preference of species i for each of its n resources is uniform ($\omega_i = 1/n$), preventing a competitive advantage for generalist species. The biological rates Y_i and X_i are written as an inverse exponential function of the body mass, M_i (Brown *et al.* 2004), $a_z M_i^{-0.25}$, with a_z the constant of the allometric relationship between the rate measured and the body mass. For the sake of simplicity we assume identical allometric constants among producers, and consider only two consumer metabolism types: invertebrates and vertebrate ectotherms (values from Brose 2008; see Table 1).

5.7.2 Ecosystem assembly

During the assembly process, new colonizer species try to invade the ecosystem. We choose at random the characteristics of the new species. They have the same chance of being a producer or a consumer and of belonging to either the autotroph or the detritivore web. Their traits (body mass M and conversion efficiency ε) are drawn from the distributions given at Table 1. For each invasion trial, we compute the new interaction matrix integrating the parameters of the colonizer. We run the numerical integration with the algorithm Runge-Kutta Kash Carp of the gsl 1.15 library for C language (Galassi *et al.*

2011) until equilibrium is reached, with a maximum of 2×10^5 integration steps. We detect equilibria by comparing averages on two successive windows of 100 integration steps (some simulations have oscillating dynamics). Equilibrium is reached when the absolute difference for each compartment between successive windows is less than 10^{-7}.

A simulation starts from an empty ecosystem with $nress$ classes of inorganic nutrients. The assembly process consists of successive assembly steps, for each of which we conduct 1000 independent invasion trials, as described above, in order to compute the probability of having a successful invasion. Colonizers have all an initial small density of 10^{-3}. We consider a species extinct and remove it from the ecosystem when its density is below a threshold of 5×10^{-4} units of biomass. At the end of the 1000 trials we chose randomly one successful colonizer to join the community. The densities at equilibrium then become the initial densities for the next colonization step. The assembly process stops either when none of 1000 species is able to colonize within a single step or after having completed 2000 assembly steps.

5.7.3 Simulations

We perform two sets of simulations: firstly, we analyze the effects of ecosystem fertility and recycling on colonization success, and secondly, we explore the effects of recycling efficiency on ecosystem development and BEF relationship at different fertilities. Hence, we first run ecosystem assemblies with different fertilities, F, varying the external inorganic resource supply I from 0.02 to 20. Fertility is calculated as the total equilibrium density of inorganic resources in the empty ecosystem: $F = (I/e) \times nress$, with e the output rate and $nress$ the number of inorganic resources. For each fertility F we perform 50 simulations with recycling ($\rho = 1$), and 50 simulations with no recycling ($\rho = 0$). We record the colonization success (% of success colonization for 1000 trials) and the maximal species richness reached during the assembly process.

For the second set of simulations, we assemble the community with the first successful colonizer of each assembly step. We perform 50 simulations for each following values of recycling efficiency: $\rho \in \{0, 0.5, 0.9, 1\}$ and environmental fertilities: $F \in$

$\{2, 3, 10, 50, 100, 500, 2000\}$. We record the following metrics over time: species richness, proportion of producers and consumers, average resident body mass for either producers or consumers, total biomass (standing stock), total biomass production (quantity of biomass produced by unit of time), total productivity (quantity of biomass produced by unit of time and biomass, i.e. biomass turnover), inorganic nutrient production (sum of green arrows in Fig. 2) and detritus production (sum of brown arrows in Fig. 2).

5.7.4 Analyses

We analyze the relationship between the colonization success and species richness for different fertilities. We then focus our detailed analysis of the effects of recycling efficiency ρ on assembly process and BEF relationship at an intermediate value of fertility F (50), for which the effect of recycling on diversity is significant. We finally investigate the effects of recycling on BEF for all fertilities with the second set of simulations. We characterize the BEF relationship by the slope of the regression between either productivity, or production biomass, and species richness, over all points of the 50 replicate assemblies for a given pair of $\{\rho, F\}$. For each fertility value, we assess the effect of recycling on BEF by the slope α of the regression between this proxy of BEF relationship and recycling efficiency ρ.

5.8 RESULTS

Colonization success is greater at intermediate values of fertility with recycling than without (Fig. 3 panels b and c). In contrast, the proportion of successful colonizers does not differ with and without recycling, at low (Fig. 3 panel a) or high (Fig. 3 panel d) fertility levels. The maximal richness (reached during the assembly) is greatly increased with recycling at intermediate values of fertility (Fig. 4). Recycling has no effect on maximal species richness at very low or high values of fertility. Maximal richness saturates more

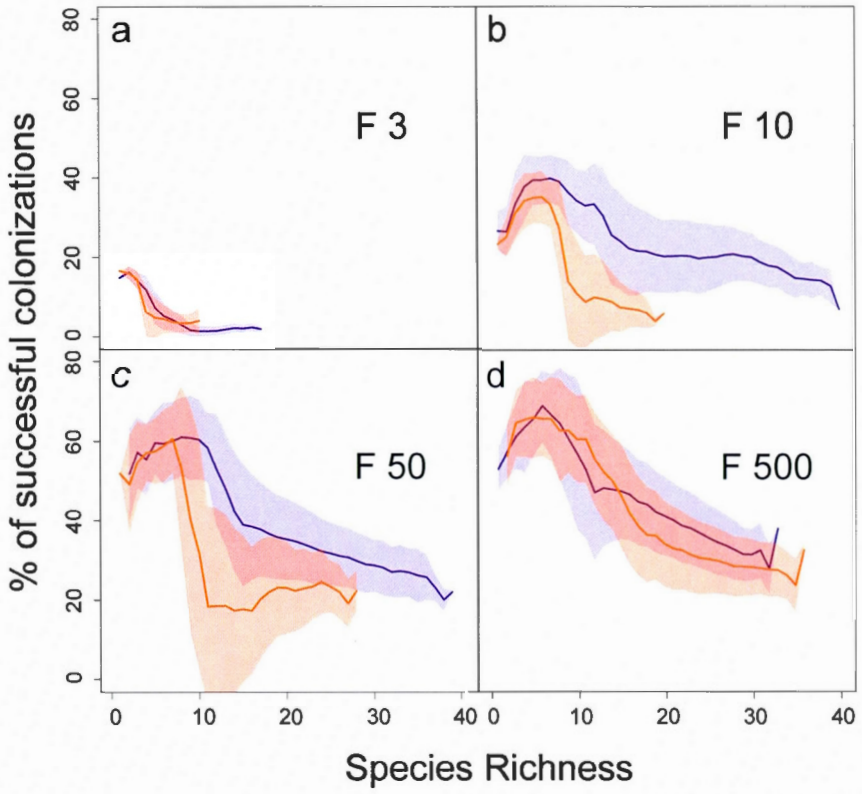

Fig. 3 Success of colonization against diversity

Percentage of successful colonizers among 1000 by level of species richness, resulting from ecosystem assemblies performed at environmental fertility F equals 3, 10, 50, 500 for panels a, b, c, d respectively, and with recycling either turned on (purple lines, $\rho = 1$) or not (orange lines, $\rho = 0$). Lines give the average over 50 simulations, and colored area the standard deviation around the average.

rapidly with fertility F when biomass is recycled. For the analysis of the effect of recycling on the assembly process and the characterization of the feedback loop, we present the results for an intermediate fertility level ($F = 50$) (Figs. 5 to 7).

Recycling efficiency, ρ, plays a crucial role in maintaining diversity (Fig. 5, panel a). Without recycling, the assembly process stops quickly because it becomes increasingly difficult for a new species to successfully establish. After only 350 steps, none of the 1000 tested colonizers is successful (Fig. 5, orange lines). Consumers that first manage to set up, finally go extinct (Fig. 5, panel b), whereas with higher recycling efficiency (Fig. 5, blue and purple lines), consumers can maintain themselves. Producers (Fig. 5c) and consumers (Fig. 5d) with smaller body masses are selected along the assembly and a lower recycling

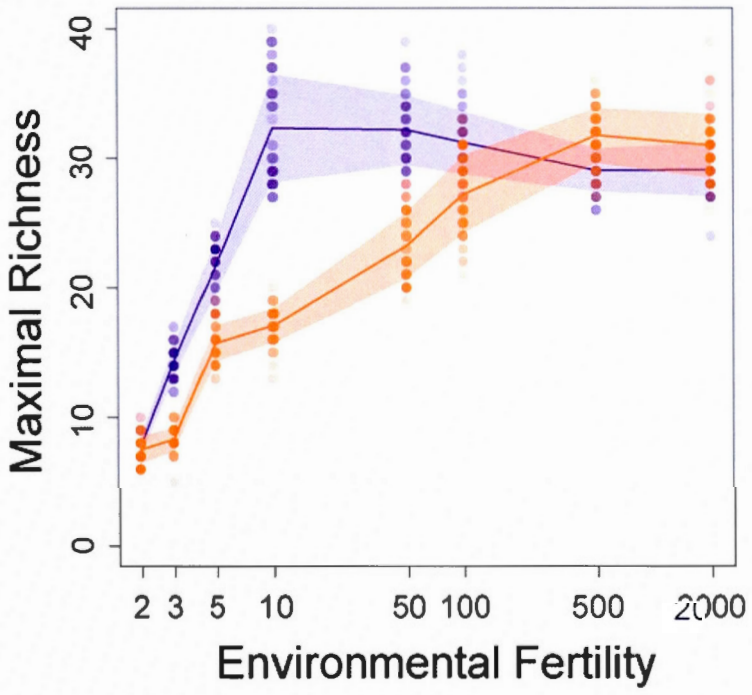

Fig. 4 Effect of recycling on fertility diversity relationship
The maximal richness reached during the assembly process, with recycling either turned on (purple lines, $\rho = 1$) or off (orange lines, $\rho = 0$), is plotted against the environmental fertility. Points give the result for one simulation. Darkness increases with the number of points of the same value. Lines give the average over 50 simulations, and colored area the standard deviation around the average.

efficiency accentuates that process. In the absence of recycling, the loss of consumer species and the selection of small body masses decrease total ecosystem biomass through time (Fig. 6 panel a). In contrast, productivity increases in all cases, independently of recycling efficiency (Fig. 6 panel b).

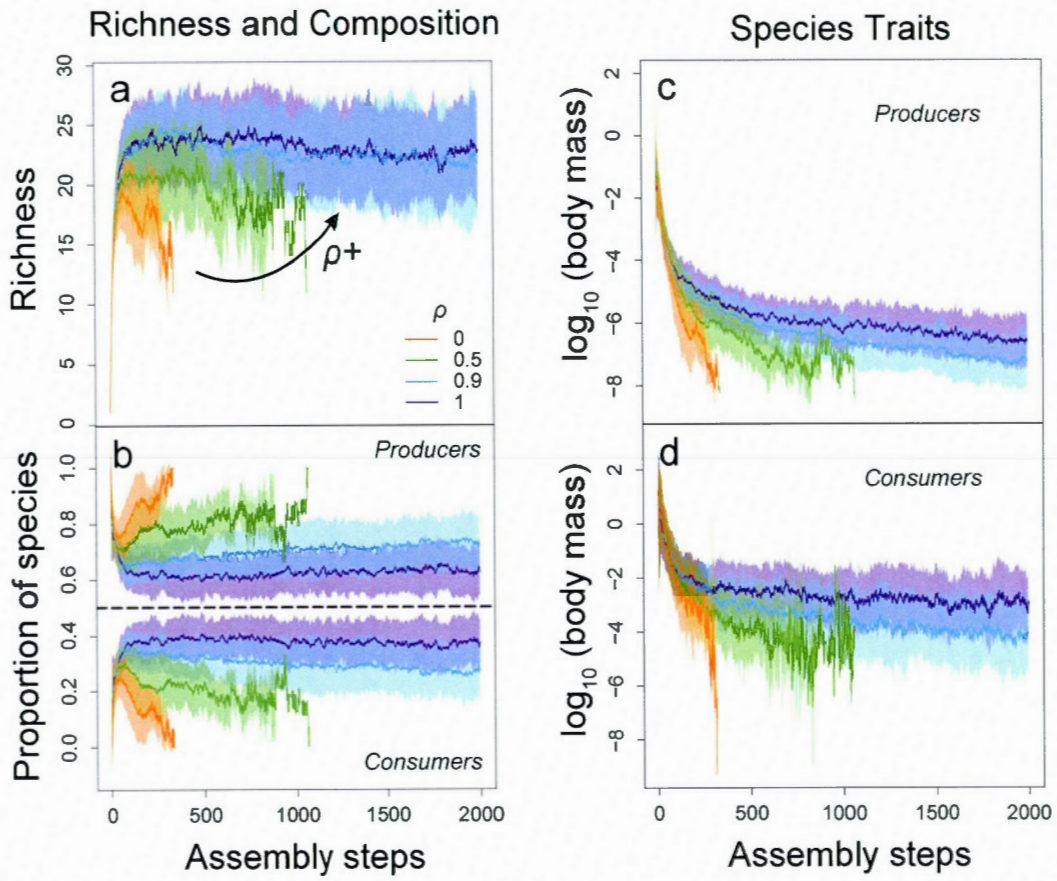

Fig. 5 Diversity and species traits variations along assembly

(a) Species richness, (b) proportions of producers and consumers, and average log10 of the specific body mass of either (c) producers, or consumers (d) are plotted along the assembly process. Orange, green, blue and purple colors refer to recycling efficiency: $\rho = \{0, 0.5, 0.9, 1\}$ respectively. Lines give the average over 50 simulations, and colored area the standard deviation around the average

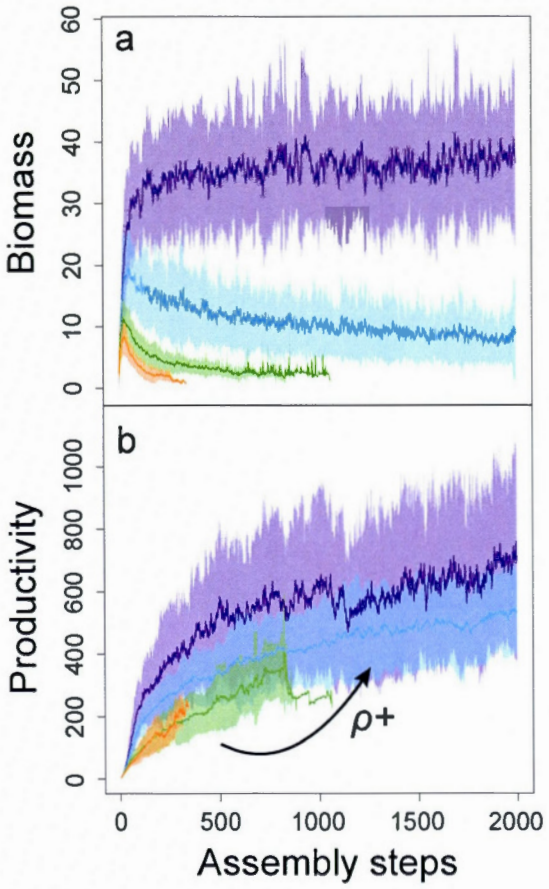

Fig. 6 Ecosystem functioning variations along assembly

(a) Total biomass (standing stock), and (b) total productivity (production of biomass by unit of biomass: $L^{-2}.T^{-1}$) are plotted along the assembly process. Orange, green, blue and purple colors refer to recycling efficiency: $\rho = \{0, 0.5, 0.9, 1\}$ respectively. Lines give the average over 50 simulations, and colored area the standard deviation around the average.

Biomass and productivity variations along the food web assembly process generate a positive relationship between species richness and ecosystem functioning (Fig. 7 panels a and b). The strength of this relationship (regression slope) increases with recycling efficiency. Biomass saturates rapidly with diversity, and even decreases slightly at intermediate diversity when recycling is absent (Fig. 7, panel a). Conversely, productivity

saturates only with inefficient recycling (Fig.7 panel b). Similar results are obtained with biomass production (Appendix A). We also analyze the relationship between nutrient and detritus production against productivity in order to characterize the reciprocal feedback between biodiversity and ecosystem functioning (Fig. 7 panels c and d). Both increase with productivity and saturate at a level depending strongly on recycling efficiency: above a certain threshold of productivity, increasing the recycling allows a greater production of inorganic nutrients and of detritus, the basal resources of the two food webs, for the same level of productivity. Therefore, the total ecosystem fertility, defined as the total of inorganic nutrient inputs from both external supply and recycling, increases with productivity, and thereby with diversity.

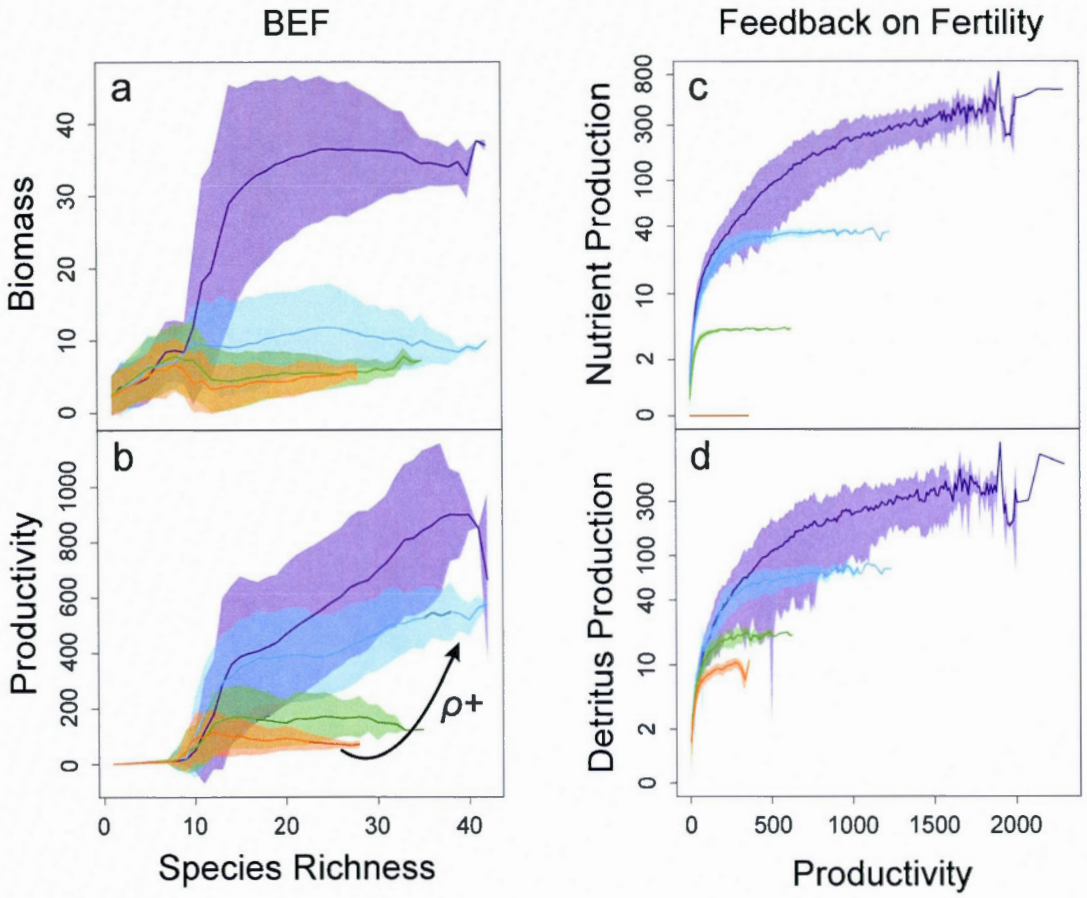

Fig. 7 BEF relationship and feedback on fertility through recycling

(a) Total biomass (standing stock), and (b) total productivity (production of biomass by unit of biomass: $L^{-2}.T^{-1}$) are plotted against species richness. And (c) nutrient production, and (d) detritus production are plotted against total productivity. Orange, green, blue and purple colors refer to recycling efficiency: $\rho = \{0, 0.5, 0.9, 1\}$ respectively. Lines give the average over 50 simulations (but obviously, not all simulations reach the maximal richness), and colored area the standard deviation around the average.

Beyond above results for an intermediate fertility, we find a positive BEF relationship for all fertilities simulated at all recycling rates, for both biomass production and productivity metrics (Fig. 8a and 9a, points). The effect of recycling on the species richness-productivity relationship is null at very low fertility ($F = 2$) but positive in all other cases (Fig. 8a, slope of the lines). Recycling increases the positive effect of diversity on productivity up to intermediate fertilities, but has a lesser effect at high fertilities, for which the BEF relationship is already strongly positive without recycling (Fig. 8). At very low fertility, diversity has little effect on productivity, regardless of the recycling efficiency. In contrast, the positive effect of recycling on diversity – biomass production relationship increases drastically with fertility (Fig.9).

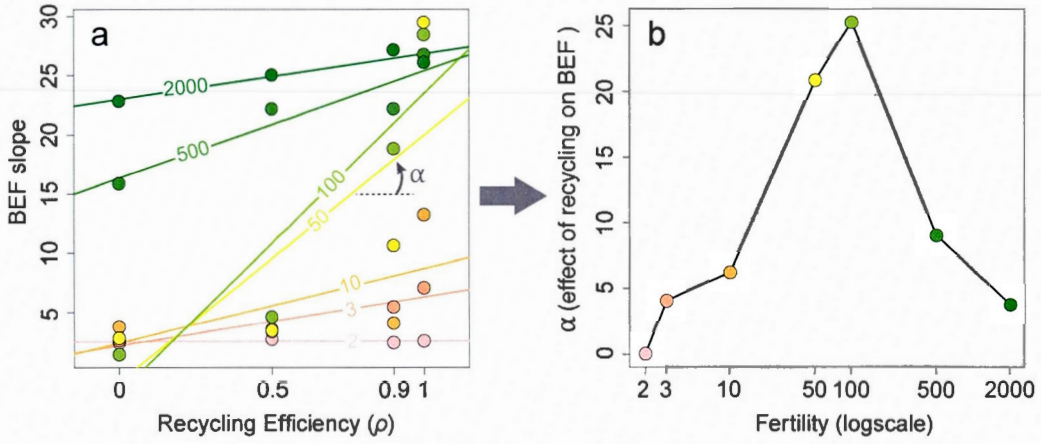

Fig. 8 Interaction between recycling, environmental fertility and BEF relationship
Points in panel a shows the slope of regressions made on all biodiversity – productivity points (Figure 7b) along 50 replicate assembly sequences, for a given environmental fertility F (colors), and a given value of recycling efficiency ρ (X-axis). Productivity is the turn over rate of biomass ($L^{-2}.T^{-1}$ dimension). Lines in panel a are regressions made on these points for the different fertilities (values indicated in color within the graph). The slope α of these regressions represents the effect of increasing recycling on the BEF relationship. We plotted α against fertility in panel b.

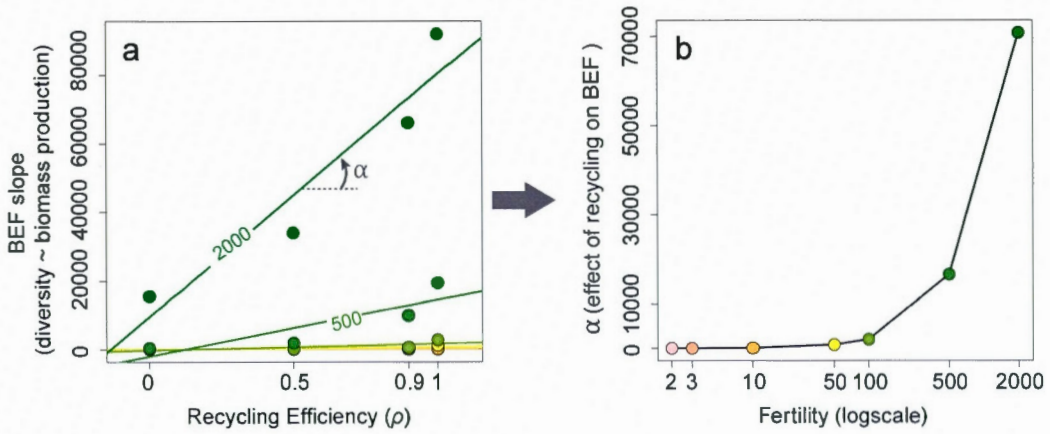

Fig. 9 Interaction between recycling, environmental fertility and BEF relationship when the proxy of ecosystem functioning is biomass production

Points in panel a shows the slope of regressions made on all biodiversity – biomass production points along 50 replicate assembly sequences, for a given environmental fertility F (colors), and a given value of recycling efficiency ρ (X-axis). Biomass production is the quantity of biomass produced by unit of surface and time ($M.L^{-2}.T^{-1}$ dimension). Lines in panel a are regressions made on these points for the different fertilities (values indicated in color within the graph). The slope α of these regressions represents the effect of increasing recycling on the BEF relationship. We plotted α against fertility in panel b.

5.9 DISCUSSION

We develop a Bioenergetic Ecosystem Assembly model (BEA model) in which we study the effect of recycling on ecosystem assembly process and the resulting Biodiversity Ecosystem Functioning (BEF) relationship. Our results show the critical role that recycling efficiency can play in ecosystem assembly through a facilitative effect on colonization success. Efficient nutrient cycling enhances coexistence along the assembly process and improves ecosystem functioning. We also find that recycling has a globally positive effect on the BEF relationship. However, the strength of this effect varies with fertility and follows either a hump-shaped or an exponential relationship, depending on the proxy

chosen for ecosystem functioning (i.e. productivity or biomass production). We discuss these results below and then propose future research directions.

Our model analysis suggests that the assembly process selects species with smaller body masses (Figs. 5c and 5d). Previous work (Gounand *et al.*, submitted manuscript, thesis chapter 3) has shown that community assembly progressively excludes large species at the basis of the food web through competitive interactions. Species with small body masses are more competitive than large ones because of their greater productivity (mass is inversely correlated with productivity; Brown et al. 2004), which enables them to stand higher predation pressure and win the apparent competition (Holt and Lawton 1994, Holt *et al.* 1994, 2001, Chase *et al.* 2002, Chesson and Kuang 2008). Such "ecological selection"[2] of smaller body masses is observed, for instance, in benthic communities under increasing predation pressure (Blumenshine *et al.* 2000), and small sizes have been shown to act as a refuge for bacteria to escape grazing from flagellates (Boegnik *et al.* 2004).

Consumer body mass also sharply decreases along ecosystem assembly, probably due to both competitive exclusion and the range of prey available (large consumers feed on large preys, which become scarcer along the assembly (Fig. 5d). Moreover, the decrease in the average producer body mass results in higher primary productivity (more productive species; Fig. 6b). As a consequence of more rapid matter flows within the food web, ecosystems lose more biomass through time in case of inefficient recycling (Fig. 6a). This biomass loss drives the extinction of consumers along the assembly process all the more quickly that recycling is less efficient (Fig. 5b). The subsequent loss of diversity (Fig. 5a) strengthens intraspecific competition and accelerates the selection of smaller body masses (Figs. 5c and 5d). This feedback loop between traits, ecosystem functioning and food web structure finally reduces colonization success under low recycling efficiency, and stops the assembly process.

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[2] *sensu* thesis chapter 3; "ecological selection" refers to a selection process driven by species interaction without considering any evolution mechanism such as speciation or adaptation.

A positive relationship between diversity and ecosystem functioning was observed over the course of ecosystem assembly. This positive BEF relationship is not directly comparable to the observations in field experiments (*e.g.* Hector *et al.* 1999, Tilman *et al.* 1997a). Our BEF relationships emerge from both the progressive filling of resource niches along assembly, ending with a decrease of colonization success (not shown), and from an increase of species productivity due to ecological selection. This situation contrasts with experiments conducted with a fixed, tightly controlled pool of coexisting species and does not account for successive species replacement (but see Sandau *et al.* 2014). Both mechanisms induce a better use of available resources, either by filling niches or by better exploiting the resource of a given niche, and belong to what has been called niche complementarity (Loreau *et al.* 2001).

In field experiments, a better "niche filling" makes species mixtures more productive than the best monoculture (Hector *et al.* 1999, Tilman *et al.* 2001, Gross *et al.* 2007). In our simulations, the different classes of resources and detritus provide different niches for producers, which are progressively filled through time and increase biomass production (Fig. 6a). Novel niches for consumers also emerge along the assembly with a wider range of potential preys (Wooton 2002, White *et al.* 2006, Bakker *et al.* 2006). The distribution of prey body mass determines the diversity of these niches at a given time, and the potential for complementarity among consumers to occur. Selection however acts against niche construction by restricting body mass ranges to smaller values during the assembly. The subsequent gain of productivity with smaller body masses increases the exploitation of basal resources and finally benefits overall biomass production (Appendix A) as well as the standing stock, as long as it is not detrimental to consumer persistence (efficient recycling). Moreover, ecological selection occurring in assembly processes erases the sampling effect found in early times of succession (Fargione *et al.* 2007).

In addition, a more efficient recycling allows a better functioning at high diversity, by increasing nutrient and detritus productions, fuelling both the autotroph and the detritivore food webs (Figs. 7c and 7d). Indirect facilitation emerges from this feedback of diversity on fertility through recycling and favors the installation of new colonizers at high diversity

(Fig. 3b and 3c). Nutrient retention increases with species diversity, thereby promoting the buildup of a diverse and productive ecosystem (Dybzinski *et al.* 2008). Direct facilitation is common between plants (Callaway and Walker 1997, Van Der Putten 2009, Bonanomi *et al.* 2011), and commonly involves the improvement of the local environment by shading or water or nutrient retention (Holmgren *et al.* 1997, Kéfi *et al.* 2007). Emerging facilitation is also often found in complex food webs, where indirect interactions could combine and reverse antagonistic interactions such as predator-prey and host-parasite interactions (Montoya *et al.* 2009), and possibly lead to a trophic complementarity (Poisot *et al.* 2013). In our model, the uniform redistribution of detritus and nutrient productions among resources mimics facilitation mechanism found with nurse plants (Tewkesbury and Lloyd 2001) by allowing a productive species to supply other niches, then to facilitate the setting up of other species, and hence reinforcing the effect of complementarity.

Overall, we find that recycling has a positive effect on the BEF relationship, but that the magnitude of its effect depends on fertility (Figs 3, 4, 8 and 9) and on the metric used for ecosystem functioning (Mittelbach *et al.* 2001). The effect of nutrient cycling on the strength of the diversity-productivity relationship follows a hump-shaped relationship with fertility, whereas it follows a positive relationship for the diversity-production (Figs. 8b and 9b). Overall, the effect of nutrient cycling remains weak when the environment is very poor because only a few primary producers can settle in the ecosystem. The scarcity of nutrients does not allow the production of enough biomass for consumer colonization, even with nutrient retention via recycling. With a little more fertility, recycling enables the establishment of secondary producers as well as improves the BEF relationship via a complementarity effect. The effect of recycling on the diversity-productivity relationship is maximal at intermediate fertilities, for which the nutrient allochtonous input alone is not sufficient to maintain consumers. Subsequently, recycling improves the BEF relationship by allowing niche construction. The resulting greater species diversity leads to a greater cumulated productivity. If fertility is very high, basal resources are not limiting anymore and the effect of recycling weakens. The selection of small body masses by competitive exclusion becomes relatively independent from recycling efficiency as well as from

ecosystem productivity (not shown). Recycling has a systematically positive effect on the diversity-production relationship (Fig. 9). At high fertilities, production benefits greatly from recycling: the high total biomass (standing stocks) due to high fertilities, combined with high productivities would cause important losses of matter from the ecosystem in case of inefficient recycling.

In addition, our model produces a positive relationship (Fig. 4). Instead, along a succession in fertile ecosystems, competition for inorganic nutrients may shift to a competition for light (Huston and De Angelis 1994). This may decrease diversity such as with macro-algae dominance replacing coral reefs (Knowlton 1992) or cyanobacteria in lakes (Scheffer *et al.* 1997, Scheffer 2009). The BEA model suggests that no hump-shaped relationship between fertility and diversity is expected without a second niche axis, such as light. Other studies have shown that diversity can decrease with fertility for instance if species biomass directly affects other species' growth, such as with light (Huston and De Angelis 1994). We did not implement this mechanism in our model, in order to focus on recycling feedback loop. Nevertheless, we expect that its effect on the BEF relationship would depend on whether competition for light is won by more productive but small species protected from grazing (e.g. cyanobacteria) or less productive and larger ones, such as trees.

We included recycling for the first time into the BEF debate for complex food webs. Our BEA model shows that recycling efficiency plays a crucial role in the assembly of food webs when accounting for metabolic constraints in trophic interactions.

Further steps for studying the BEF recycling loop would consist in investigating non-linear functional responses, which involve additional coexistence mechanisms (Armstrong and McGehee 1980, Chesson 1994, Huisman and Weissing 1999, Drossel *et al.* 2004) and would likely lead to more diverse final food webs (chapter 4 of this thesis). It would also be interesting to investigate the relative role of autotroph versus detritivore webs in shaping the BEF relationship, and to compare the results with previous modeling studies on plant – decomposer interactions (Loreau 1998b, 2001). Moreover, we made the simplifying

assumption that these two webs only interact through organic matter decomposition and mineralization. However, the coupling of autotroph and detritivore webs through generalist consumers is widespread in nature (Rooney *et al.* 2006), for instance the coupling of between pelagic and benthic webs with fishes (Graf 1989, Menge *et al.* 1997, Schindler and Scheuerell 2002), and would deserve consideration in further studies involving a slight modification of the BEA model. Finally, temperature-dependence of species metabolism can easily be implemented in the BEA model (Vasseur and McCann 2005, chapter 3 of this thesis). The comparison between simulations at different temperatures may provide interesting information on the sensitivity of the recycling effect on BEF relationship to global warming.

To conclude, the BEA model succeeds in integrating food web assembly dynamics with ecosystem development and thereby enables to replace the BEF relationship in a dynamical context.

5.10 ACKNOWLEDGEMENTS

We thank Frederic Guichard and Tanguy Daufresne for early discussions, and James Caveen, Rémy Dernat and Khali Belkhir for technical help. The simulations of the project largely benefited from UQAR and ISEM computing clusters, and the Monptellier Bioinformatics Biodiversity platform (funded by the LabEx CeMEB). I.G. was supported by a MENRT grant from Ministry of Higher Education and Research of France, the Canada Research Chair Program, the Quebec Center for Biodiversity Science and by the Frontenac program (FQRNT and French consulate at Québec). D.G. and P. D.-P. were supported by the NSERC and the Canada Research Chair Program.

5.11 APPENDIX A – DIVERSITY ~ PRODUCTION RELATIONSHIP

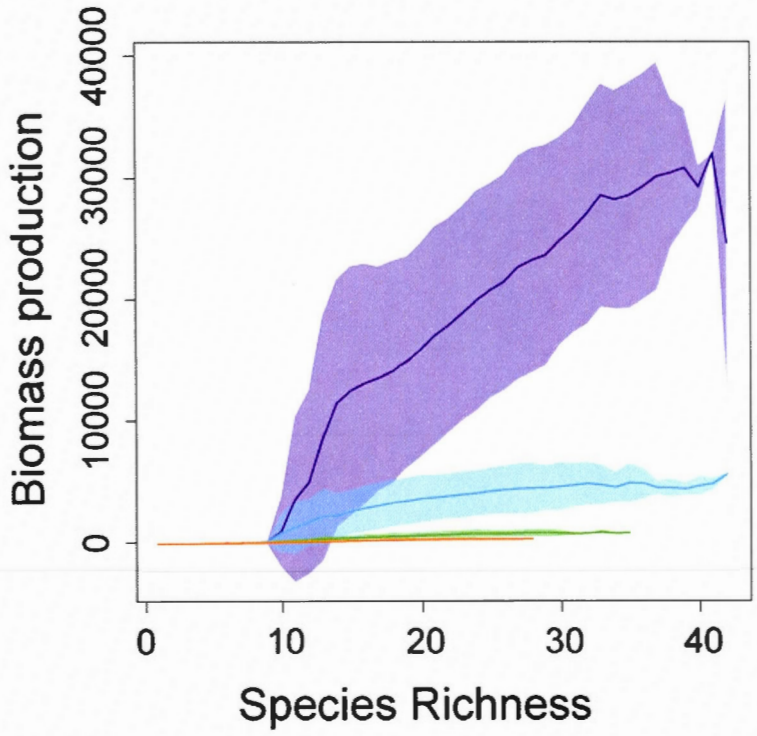

Fig. A BEF relationship with biomass production

Total biomass production ($M.L^{-2}.T^{-1}$ dimension) plotted against species richness. Orange, green, blue and purple colors refer to recycling efficiency: $\rho = \{0, 0.5, 0.9, 1\}$ respectively. Lines give the average over 50 simulations, and colored area the standard deviation around the average.

CONCLUSION GÉNÉRALE

Mon objectif dans cette thèse a été de caractériser des mécanismes d'interactions entre environnement abiotique, réseaux trophiques et fonctionnement des écosystèmes. Dans cette conclusion générale je fais d'abord le point sur ces mécanismes et sur leur originalité chapitre par chapitre. Ensuite j'explicite l'articulation des résultats entre eux, en les replaçant dans un contexte plus global. Enfin je donne des perspectives pour améliorer et poursuivre cette démarche d'intégration de l'écologie des écosystèmes et des communautés.

BILAN DES NOUVEAUX MECANISMES

Chapitre 1 – Interactions entre ressource inorganiques et stratégies de croissance

En sélectionnant des bactéries à différentes densités de populations à partir d'une population *ancêtre* unique, j'ai fait émerger différentes stratégies de croissance (figure 7) : les bactéries sélectionnées à faibles densités (en bleu) étaient caractérisées par de petites tailles de cellule, un fort taux de croissance maximal, μ_{max} (capacité à croître vite), et une forte compétitivité sur le phosphore, C_P. Les bactéries sélectionnées à fortes densités (en orange) étaient au contraire caractérisées par de plus grandes tailles de cellules, un plus faible taux de croissance maximal et une moindre compétitivité pour le phosphore. L'expérience d'évolution a montré que la relation entre compétitivité et capacité à croître vite sur des milieux pauvres en phosphore pouvait être positive, alors que l'on aurait pu s'attendre à un compromis physiologique dû à un fort besoin en phosphore de la fonction de biosynthèse (théorie du taux de croissance : Elser *et al.* 2000, Sterner et Elser 2002). En fait cette relation est fortement dépendante de la taille des cellules car plus une cellule est petite, moins elle met de temps pour se diviser (Hessen *et al.* 2010a, 2013) et plus elle est

efficace dans l'acquisition des ressources grâce à un plus grand ratio surface : volume (chez les organismes qui se nourrissent par diffusion, ou osmotrophes ; Tambi *et al.* 2009). La sélection de ces stratégies de croissance correspondait à une variation densité-dépendante de l'approvisionnement en ressources, R, dans nos traitements de sélection : les bactéries sélectionnées à faible densité ont bénéficié d'une ressource abondante et relativement

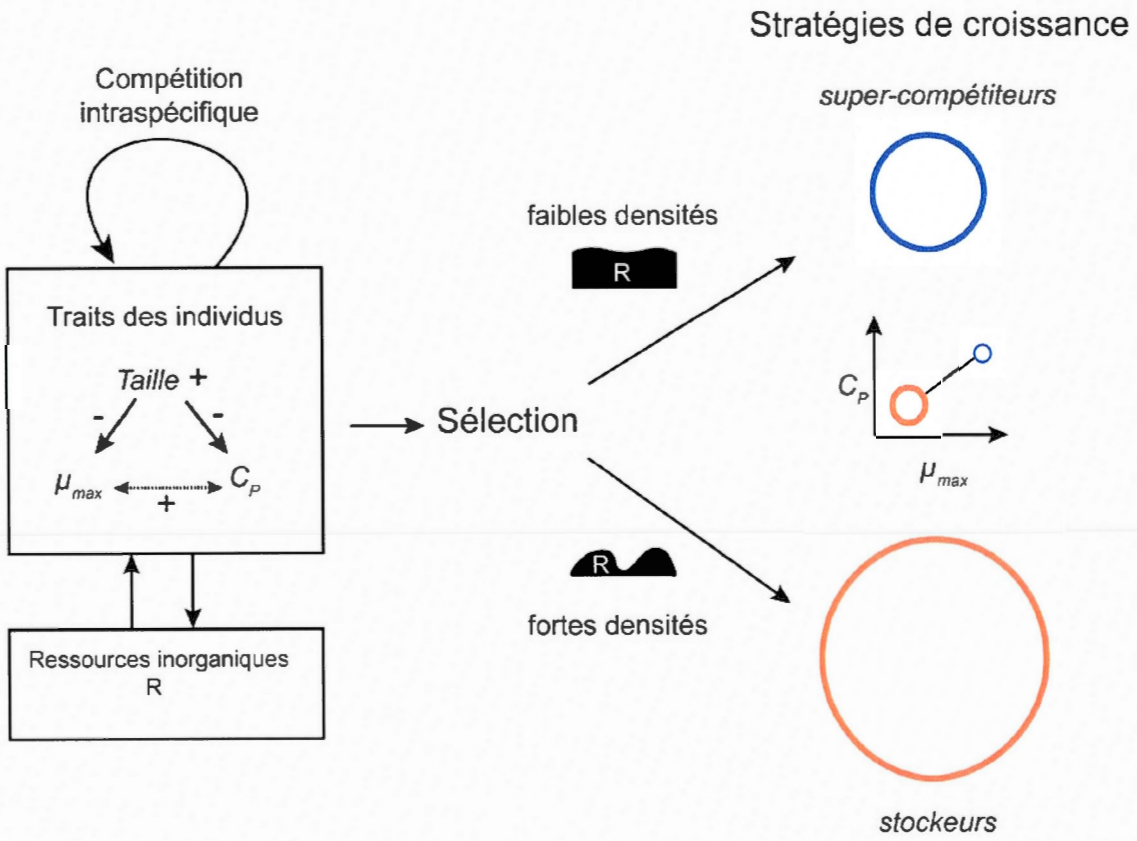

Figure 7 Sélection de stratégies de croissance selon l'approvisionnement en ressources

continue, ce qui a sélectionné des petites bactéries super-compétitrices. Les bactéries sélectionnées à forte densité ont été soumises à des périodes de disette régulières, ce qui a sélectionné des bactéries plus grosses, dont on peut faire l'hypothèse qu'elles résistent à la disette en stockant des réserves (Makino et Cotner 2004). Point important, la sélection à

forte densité menait à une plus grande diversité de tailles de cellules, suggérant une coexistence entre les *stockeurs* et les *super-compétiteurs*.

Ces résultats corroborent certains résultats de récentes études de modélisation et d'analyse de données empiriques sur le phytoplancton, qui montrent la dépendance entre taille de cellules et compétitivité pour l'azote et le phosphore, ainsi que le lien entre taille de cellule et d'approvisionnement des ressources (Litchman *et al.* 2009, Edwards *et al.* 2011). L'originalité de cette étude repose sur l'aspect expérimental. Pour la première fois, l'émergence de cette relation entre compétitivité, capacité à croître vite et taille des cellules est caractérisée grâce à un processus de sélection en milieu contrôlé. Cela permet de retirer les potentielles sources de variation (par exemple des prédateurs) pour vérifier l'origine physiologique de cette relation, et de proposer la fluctuation des ressources comme mécanisme de cette sélection de stratégies de croissance.

Chapitre 2 – Interactions spatiales entre ressources inorganiques et dynamiques plante-herbivore

Avec l'analyse du modèle de méta-écosystème, j'ai identifié une série de mécanismes permettant de comprendre l'effet combiné des flux spatiaux passifs (diffusion) et de l'enrichissement (approvisionnement en nutriments) sur la stabilité des dynamiques plantes-herbivores[3] (figure 8). La comparaison entre des flux spatiaux isolés de nutriments, détritus ou d'organismes vivants a montré que l'effet sur la stabilité dépendait de la nature vivante ou inerte du compartiment qui diffuse, qui détermine aussi la synchronisation spatiale des dynamiques (figure 8a et 8b). Ainsi, les flux de nutriments et de détritus approvisionnent en ressource l'écosystème où les producteurs sont déjà les plus abondants (celui où les nutriments sont les plus consommés), ce qui accentue l'effet déstabilisant d'un enrichissement et qui désynchronise les dynamiques (figure 8a). Les flux d'organismes vivants, au contraire, synchronisent les dynamiques en diminuant les différences spatiales

[3] La stabilité est mesurée par la partie réelle de la plus grande valeur propre de la matrice jacobienne. Les dynamiques sont considérées instables lorsqu'elles fluctuent dans le temps.

non seulement pour leur propre population, mais aussi pour leur ressource par leur activité de consommation (figure 8b). La synchronisation annule le flux net de diffusion, et tout potentiel effet sur la stabilité. Une récente étude théorique en métaécosystème montrait aussi un effet déstabilisant de la diffusion des nutriments (Marleau *et al.* 2010), mais c'est

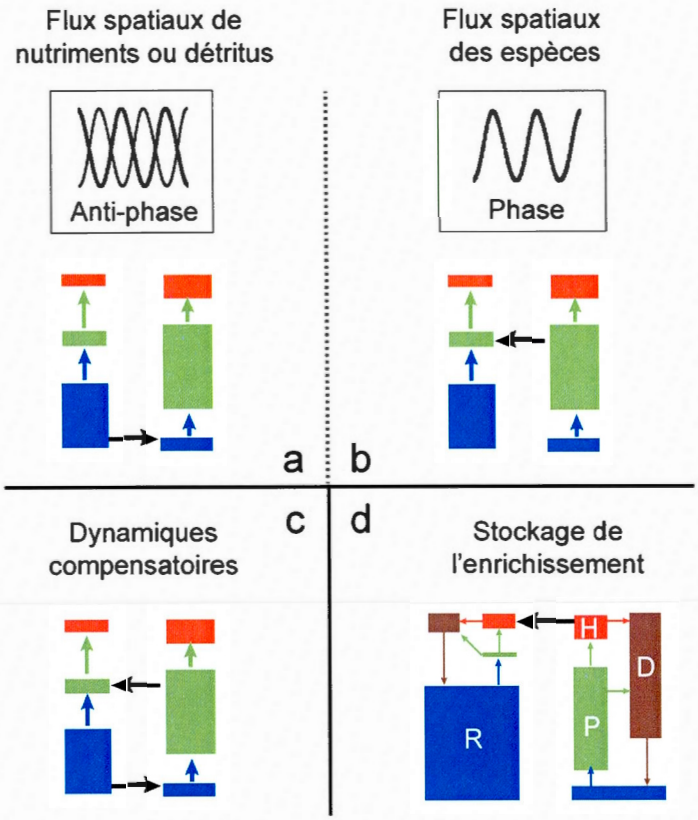

Figure 8 Flux spatiaux et stabilité en métaécosystème

Les couleurs bleu, vert, rouge, brun et les lettres R, P, H, D réfèrent respectivement à la ressource inorganique, au producteur primaire, à l'herbivore et aux détritus. Dans les panels a, b, c les détritus sont omis pour simplifier

la première fois que la comparaison est faite avec les flux spatiaux des autres compartiments de l'écosystème. Cela éclaire le rôle crucial que joue la consommation dans leurs différences d'effet sur la stabilité.

De plus dans cette étude j'identifie deux mécanismes qui diffèrent d'avec les études précédentes en méta-communautés. Premièrement, alors que l'hétérogénéité environnementale (différence de fertilité entre les écosystèmes) est montrée comme étant un facteur important de stabilisation des communautés lorsqu'elle est considérée implicitement par la capacité biotique (Hauzy *et al.* 2013), je trouve que des flux spatiaux multiples (figure 8c) combinés au recyclage renforce l'homogénéisation des écosystèmes jusqu'à pouvoir gommer totalement les différences de fertilité. Ainsi, lorsque la dynamique des nutriments est explicite, et que les écosystèmes sont bien connectés (diffusion par plusieurs compartiments), l'hétérogénéité des flux d'enrichissement ne pourra pas être un facteur de stabilisation. Deuxièmement, la prise en compte du recyclage permet d'identifier un nouveau mécanisme potentiel de stabilisation d'écosystèmes très enrichis. Pour des valeurs intermédiaires de diffusion du compartiment herbivore, les flux spatiaux peuvent mener à des états stables alternatifs dont l'un est stable, même en l'absence de toute différence entre les écosystèmes (pas d'hétérogénéité spatiale). Les flux d'herbivores venant de l'un des écosystèmes peuvent empêcher la croissance du producteur primaire de telle manière que l'excès d'enrichissement est stocké sous forme inorganique (figure 8d). La stabilité provient d'un couplage entre des écosystèmes dont la dynamique est contrôlée par les producteurs (« bottom-up controlled ») et d'autres dont la dynamique est contrôlée par les herbivores (« top-down controlled »).

Chapitre 3 – Assemblage des écosystèmes (1) : Mécanisme de Sélection écologique

L'arrivée successive des espèces dans l'écosystème induit un processus de sélection des traits des espèces résidentes que j'appelle sélection écologique (se référant à l'effet des interactions écologiques, sans mécanismes évolutifs tels que l'adaptation et la spéciation). Les événements de compétition et la pression de prédation excluent les espèces les moins efficaces à acquérir la ressource et à supporter la prédation (dans notre étude, l'herbivorie). L'analyse de ce processus dans un modèle bioénergétique d'assemblage d'écosystème m'a

de permis de caractériser le mécanisme en m'appuyant sur une étude analytique de modules simples. L'identité des traits sélectionnés durant l'assemblage de communautés de producteurs primaires, dépend beaucoup de la manière de représenter la biologie des espèces. Cette sensibilité s'estompe dès que des herbivores sont inclus. Un résultat général de l'étude est que la pression d'herbivorie conduit à sélectionner des producteurs primaires de plus en plus petits au cours de l'assemblage. Les producteurs primaires les plus gros sont néanmoins invulnérables, car aucun herbivore n'était assez gros pour les consommer.

De plus, comme le modèle bioénergétique permet d'inclure la dépendance du métabolisme à la température, j'ai pu documenter comment celle-ci agissait sur la sélection écologique en comparant des assemblages réalisés à différentes températures. L'effet de la température sur la taille des organismes (ou leur masse) implique généralement des impacts sur le développement des individus (Daufresne *et al.* 2009), qui ne sont pas pris en compte ici. Dans le modèle, la température agissait de la même manière sur toutes les espèces, par l'application d'un facteur multiplicateur identique au niveau des taux biologiques. Malgré cette simplification, je détecte que la température affecte profondément la distribution des

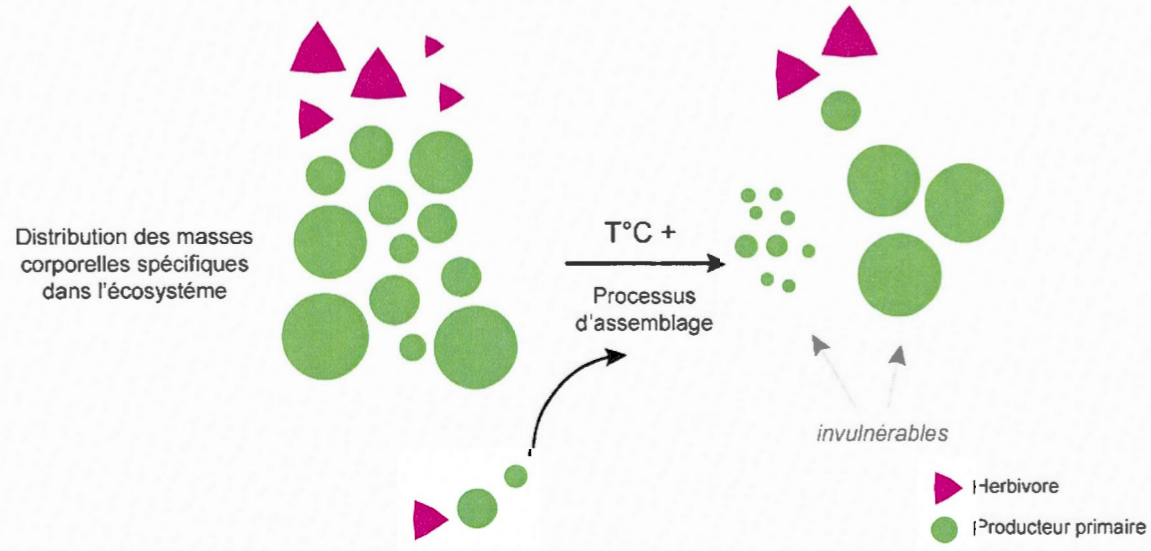

Figure 9 Sélection écologique et effet de la température

tailles des organismes et la structure du réseau trophique (figure 9). Une plus forte température accélère les flux bioénergétiques (productivité / turnover de la biomasse) mais diminue la biomasse des producteurs primaires à l'équilibre en l'absence d'herbivores. Ainsi les petits herbivores (ceux qui mangent les petits producteurs primaires) n'arrivent pas à s'installer car ils n'ont pas assez à manger. Cela rend les tout petits producteurs invulnérables à l'herbivorie, comme le sont aussi les très gros (figure 9). Ce changement de proportions des producteurs vulnérables entraîne une compétition accrue pour l'exploitation des ressources, entre producteurs invulnérables d'une part, et entre herbivores d'autre part, qui ont chacun moins de ressources à se partager. Cela a deux effets : une renforcement de la sélection écologique pour des espèces ayant une grande efficacité de conversion de la biomasse, et une diminution de la proportion des gros producteurs par rapport aux petits, eux aussi invulnérables, à cause de la moins grande compétitivité des grands organismes pour l'exploitation des ressources. Cette étude analyse en détail pour la première fois ce mécanisme par lequel la température peut indirectement influencer la structure des réseaux trophiques.

Chapitre 4 – Assemblage des écosystèmes (2) : Effet du timing d'assemblage

Dans ce chapitre, j'ai testé pour la première fois l'effet du timing de l'assemblage, notamment le nombre d'espèces arrivant par unité de temps (vitesse d'assemblage), sur la diversité finale des réseaux trophiques, en contrôlant l'effet de l'ordre dans lequel les espèces arrivent. Cet effet qualitatif dépend fortement de la réponse fonctionnelle des espèces lorsqu'on considère les écosystèmes arrivés à l'équilibre (figure 10), mais pas si on considère que la dynamique de colonisation se poursuit indéfiniment (état transitoire).

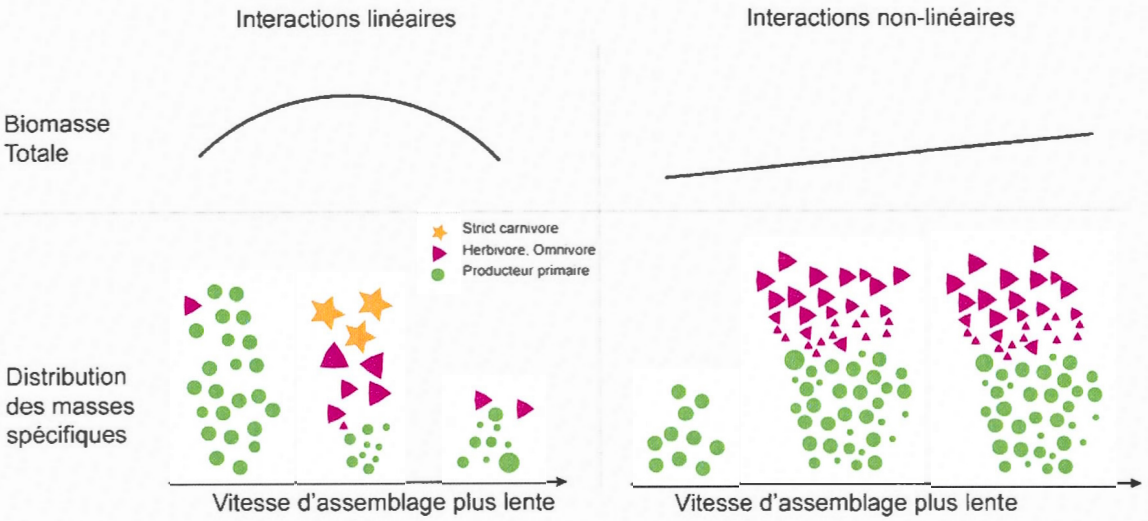

Figure 10 Effet de la vitesse d'assemblage sur la sélection des masses et la biomasse

Avec des réponses fonctionnelles linéaires (figure 10, à gauche), la diversité décroît quand les espèces arrivent plus lentement car la compétition a le temps d'exclure les espèces les moins compétitives. Quand l'assemblage est très rapide (ou qu'il est simultané), les consommateurs ne peuvent pas s'installer à cause des biomasses initiales trop faibles de leurs proies. La grande diversité tient alors à une très grande lenteur des dynamiques locales due à l'extrême similarité des espèces restantes (Gravel *et al.* 2006, Scheffer et Van Nes 2006), ou à la présence possible de grosses espèces au métabolisme très lent. L'écosystème présente une plus grande complexité trophique pour des vitesses intermédiaires d'assemblage. Celles-ci permettent à des interactions indirectes de se mettre en place et d'empêcher éventuellement les compétiteurs les plus faibles d'être exclus. Ainsi plus de proies sont disponibles, rendant possible l'installation des espèces des niveaux trophiques supérieurs (*e.g.* les carnivores : figure 10, les étoiles). Cette diversité des consommateurs accentue le mécanisme de sélection écologique vers des producteurs primaires plus petits et plus productifs, ce qui bénéficie à la biomasse totale dans l'écosystème (figure 10, ligne noire à gauche).

Avec des réponses fonctionnelles non linéaires (figure 10, à droite), la distribution des masses des espèces semble insensible à la vitesse d'assemblage (excepté si les consommateurs ne peuvent s'installer, comme dans le cas d'un assemblage simultané). La distribution des masses est plus compacte, peut-être à cause de plus faibles biomasses à l'équilibre qui limiteraient l'écart entre les masses des proies et des prédateurs. Quoiqu'il en soit, cela augmente la connectance du réseau et limite probablement les extinctions secondaires et la perte de diversité quand la vitesse de l'assemblage est plus lente. Néanmoins, des vitesses d'assemblage plus lentes renforcent légèrement le processus de sélection écologique vers de plus petits et plus productifs producteurs primaires, ce qui bénéficie à la biomasse des consommateurs et à la biomasse totale de l'écosystème.

Chapitre 5 – Assemblage des écosystèmes (3) : Recyclage et boucle d'interaction entre biodiversité et fonctionnement des écosystèmes

En intégrant la boucle du recyclage dans le processus d'assemblage, j'ai pu analyser comment la diversité et le fonctionnement des écosystèmes rétroagissent l'une sur l'autre au cours du développement de l'écosystème. Je montre comment l'efficacité du recyclage influence la relation BEF en fonction de la fertilité intrinsèque de l'écosystème (figure 11). La diversité augmente d'autant plus la production de biomasse que le recyclage est efficace car plus de matière est conservée dans l'écosystème. Par contre, l'effet positif du recyclage sur la relation entre diversité et productivité (*i.e.* turn-over de la biomasse) est maximal pour des fertilités intermédiaires (figure 11, à droite). Cette relation s'explique par l'effet du recyclage sur la structure du réseau. Pour des fertilités intermédiaires, la conservation de la biomasse à l'intérieur de l'écosystème augmente avec l'efficacité du recyclage de telle manière que des consommateurs persistent dans l'écosystème, qui ne le pourraient pas autrement à cause du processus de sélection écologique vers de plus petites masses à la base du réseau. Ceci permet d'atteindre grâce au recyclage une plus grande diversité au cours de l'assemblage, et par conséquence une plus grande productivité cumulée. Pour des petites ou de grandes fertilités, le recyclage n'a que peu d'effet sur la relation diversité –

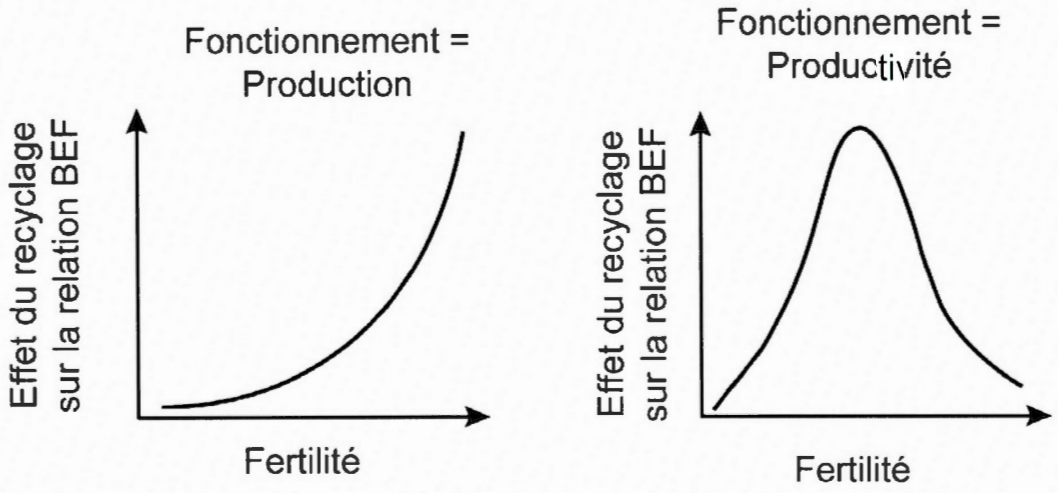

Figure 11 Interaction entre effet du recyclage et fertilité sur la relation BEF

productivité, respectivement parce que l'écosystème est trop infertile même avec le recyclage pour permettre l'installation des consommateurs, ou parce la grande fertilité permet aux consommateurs de s'installer même en l'absence de recyclage.

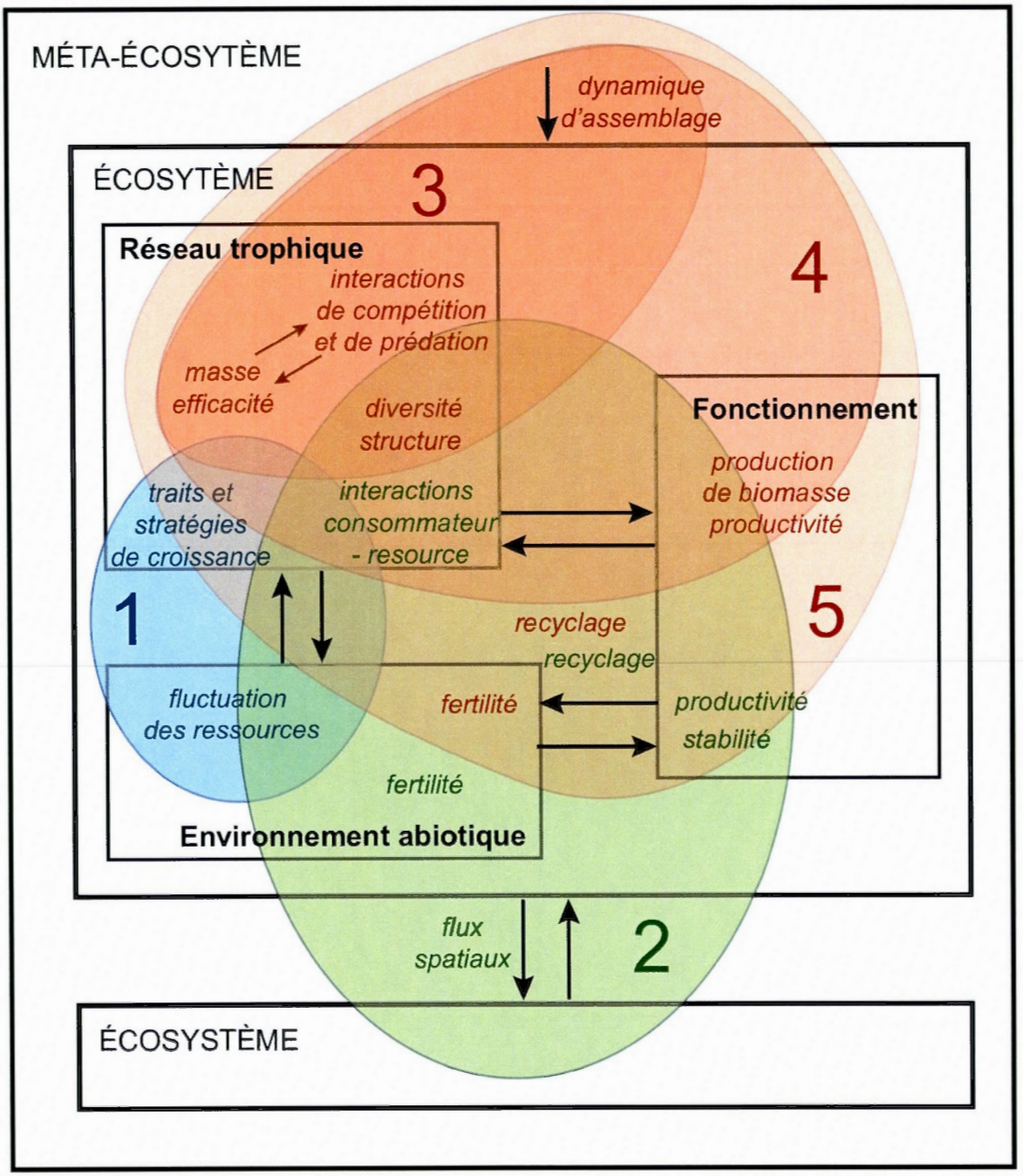

Figure 12 Liens entre les chapitres

ARTICULATION ET MISE EN CONTEXTE DES RESULTATS

Les chapitres s'articulent sur une échelle d'organisation croissante, liant les traits des espèces au fonctionnement de l'écosystème. La figure 12 les replace dans le cadre conceptuel de départ, par des bulles de couleurs qui englobent leur domaine d'application (les grands chiffres réfèrent aux numéros des chapitres). Dans le chapitre 1 j'illustre une interaction entre fluctuation/disponibilité des ressources et traits des espèces (bulle bleue). Dans le chapitre 2, je montre comment fluctuation/disponibilité des ressources interagissent avec une chaîne trophique simple, dans un contexte spatialisé, et comment cette interaction détermine la stabilité des écosystèmes au niveau local et régional (bulle verte). Dans les chapitres 3 à 5 (bulles marron) j'analyse progressivement comment les traits des espèces, sélectionnés par leurs interactions au cours du processus d'assemblage, agissent sur la structure de réseaux trophiques plus complexes (chapitre 3 à 5), sur le fonctionnement des écosystèmes (chapitre 4 et 5). Je montre au final comment diversité et fonctionnement interagissent par le biais du recyclage au cours du développement des écosystèmes (chapitre 5).

Dans l'expérience d'évolution (chapitre 1), les transferts de population dans du nouveau milieu peuvent être assimilés à des perturbations qui détruisent une proportion de la population. Ainsi, ce régime de perturbation, associé à la croissance des organismes qui consomme les ressources, produit aussi une fluctuation des ressources qui devient un moteur de sélection pour les traits des organismes. La sélection observée opère probablement par un mécanisme de sélection écologique, comme examinée au chapitre 3 au niveau des espèces. Les individus les plus adaptés à une situation persistent, se multiplient et leurs traits se propagent dans la population. Si les perturbations sont sévères et maintiennent un haut niveau de ressource (comme avec les transferts de petits volumes), on obtient une faible diversité avec de petites bactéries très semblables, rapides à croître et compétitives. Si les perturbations sont peu sévères et laissent la croissance des populations réduire drastiquement les ressources, alors la dominance des super-compétiteurs décroît et on obtient des populations plus diverses, où notamment des bactéries ayant

vraisemblablement une stratégie de stockage des ressources peuvent persister. Ces interactions entre ressources et stratégies de croissance des espèces, et la diversité ou spécialisation des stratégies de croissance qui en résulte au sein d'une population, se répercuteront sur les interactions de cette population avec les autres espèces, au sein du réseau trophique.

L'interaction entre fluctuation des ressources et croissance des espèces peut aussi être envisagée selon ses effets purement dynamiques, sans considérer la variation des traits des espèces (chapitre 2). Dans un contexte de changements globaux, les phénomènes d'enrichissements en nutriments sont très communs, et aussi bien localisés (*e.g.* lessivage de fertilisants) qu'à grande échelle (*e.g.* déposition atmosphérique). L'étude de leurs conséquences sur des paysages fragmentés (méta-écosystèmes) montre que la stabilisation des effets d'enrichissement repose sur la structure de la connexion entre les écosystèmes et pas seulement sur l'intensité des flux spatiaux. On peut s'attendre à ce que deux écosystèmes uniquement connectés par des flux de matière inorganique, par exemple si les espèces sont très peu mobiles ou empêchées de se déplacer par des barrières physiques, soient plus sensibles à l'enrichissement et leurs populations plus instables. Si leur connexion se fait en priorité par les herbivores, avec des flux modérés, la stabilisation d'effets d'enrichissement est plus probable. Elle pourra impliquer une asymétrie spatiale des types de régulation, avec certains écosystèmes où ce sont les producteurs primaires qui déterminent le fonctionnement de l'écosystème, couplés avec d'autres où l'influence de l'herbivorie prédomine, limitant la croissance des producteurs primaires.

Les trois derniers chapitres analysent les mécanismes du développement des écosystèmes. Ils peuvent se resituer dans un contexte global où les écosystèmes sont constamment perturbés et se reconstruisent à partir de la migration d'espèces venant de l'extérieur. Nos résultats suggèrent que dans un contexte où les interactions sont essentiellement structurées par la taille des organismes (les plus gros mangeant plus petits qu'eux), le processus d'assemblage conduit globalement à un phénomène de sélection écologique vers des tailles plus petites d'organismes à la base du réseau trophique. Cette sélection peut être tempérée, par exemple si des espèces basales peuvent échapper à la

consommation grâce à une taille plus grande (chapitre 3). Globalement, cela améliore le fonctionnement de l'écosystème, dans la mesure où la diminution des tailles ne provoque pas un effondrement des populations de consommateurs (chapitre 5). Ces extinctions, possibles dans des écosystèmes peu à modérément fertiles, peuvent néanmoins être évitées par un recyclage local efficace de la biomasse (chapitre 5). En définitive, la relation entre biodiversité – fonctionnement des écosystèmes se construit au fil du processus d'assemblage et au fil des changements de composition et de structure du réseau trophique qu'il provoque. Ces changements peuvent être modulés par le timing d'arrivée des espèces dans l'écosystème (chapitre 4), par la température (chapitre 3) et par l'interaction entre la fertilité de l'écosystème et l'efficacité du recyclage local (chapitre 5). Dans un contexte de changements globaux, ces résultats suggèrent entre autres que le réchauffement climatique pourrait avoir des conséquences indirectes importantes sur la structure des réseaux trophiques, sur la force des interactions de compétition dans les réseaux (chapitre 3), et donc par ricochet sur le fonctionnement des écosystèmes (chapitres 4 et 5).

BILAN ET PERSPECTIVES

Dans l'ensemble, ce travail permet de faire de nouveaux ponts entre écologie des écosystèmes et écologie des communautés, et plus largement de créer un espace de dialogue entre les différentes disciplines qui construisent une écologie plus intégrative : écologie stœchiométrique, théorie métabolique de l'écologie, méta-écosystèmes, assemblage des communautés, et chapeautant le tout, réflexion globale sur la relation entre diversité et fonctionnement des écosystèmes. Mon approche théorique est à mi-chemin entre des modèles très simples, éventuellement trop théoriques pour faire le lien avec les observations empiriques, et les modèles systèmes-centrés, qui peuvent faire des prédictions mais qui ne sont utilisables que dans un contexte très précis et particulier. Dans cette thèse, j'ai cherché à garder une perspective multi-systèmes, tout en prenant en compte des interactions complexes. Je me suis focalisée sur la compréhension de mécanismes qui lient les différentes échelles d'organisation des écosystèmes, et que je pense fondamentaux pour comprendre les interactions entre diversité biologique, ressources inorganiques et fonctionnement des écosystèmes.

De nombreuses perspectives s'ouvrent à ce travail. D'abord du point de vue du chapitre expérimental, l'étude de la relation entre fluctuation des ressources et stratégies de croissance chez les bactéries pourrait être approfondie en l'abordant en sens inverse : plutôt que de sélectionner des bactéries plus ou moins rapides et de regarder leur compétitivité pour des ressources essentielles, qu'adviendrait la relation si on sélectionnait des bactéries sur des milieux plus ou moins appauvris en azote ou en phosphore ? En résulterait-il des taux de croissance différents ? Différentes tailles de cellules seraient-elles aussi sélectionnées ?

Beaucoup de questions m'aiguillonnent aussi à l'issue du travail de modélisation, notamment pour poursuivre l'intégration de ces résultats. Je suis convaincue que le modèle Bioénergétique d'Assemblage d'Écosystèmes (BEA) développé dans cette thèse est un

outil formidable pour y répondre et élucider d'autres mécanismes intervenant dans la construction et le fonctionnement des écosystèmes.

Parmi ces questions, je serais très curieuse de savoir comment le mécanisme déstabilisant du « paradoxe de l'enrichissement » agit dans un contexte d'assemblage progressif de l'écosystème. Notamment, comment la fertilité modifie-t-elle la diversité des écosystèmes assemblés ? Le paradoxe de l'enrichissement compromet-il l'installation des consommateurs et appauvrit-il la complexité trophique des écosystèmes ? Est-ce que cela augmente la probabilité d'avoir des états stables alternatifs ? Est-ce qu'enfin l'effet d'enrichissement pourrait être limité par un vitesse d'assemblage plus rapide ?

Le chapitre 4 m'interroge sur l'impact de la réponse fonctionnelle sur les mécanismes de coexistence entre espèces et sur la diversité. Il suggère que des diversités plus importantes pourraient être atteintes dans les assemblages réalisés pour le chapitre 5[4]. Nos premiers résultats sur la relation BEF – recyclage sont obtenus avec des réponses fonctionnelles linéaires. Ils pourraient être approfondis en les comparant avec ceux obtenus avec des réponses fonctionnelles non-linéaires. Le chapitre 4 souligne aussi l'importance de la vitesse d'assemblage pour la structure des écosystèmes. Il serait intéressant d'étudier comment cette vitesse, ou l'arrivée groupée des espèces, peuvent éventuellement influencer la relation BEF – recyclage. Cette relation pourrait aussi être examinée sous la perspective du réchauffement climatique, en intégrant la température dans le travail réalisé au chapitre 5. Les résultats suggèrent que l'importance du recyclage devrait être accrue si la température augmente la force de la sélection écologique, comme au chapitre 3.

Enfin, un vaste champs de recherche s'ouvre en étendant la perspective d'assemblage aux méta-écosystèmes : Comment l'assemblage de deux écosystèmes se synchronise-t-il par le biais de la dispersion entre aux ? Persiste-t-il entre eux des différences de structures et de fonctionnement issues d'effets de contingences historiques durant l'assemblage (et pour quels taux de dispersion) ? Comment cet assemblage de deux écosystèmes couplés pourrait-il être affecté par une différence de fertilité intrinsèque entre les écosystèmes ?

[4] Les simulations du chapitre 5 ont été faites en début de thèse. Les chapitres 3 et 4 ont été réalisés ensuite pour comprendre le processus d'assemblage de façon plus poussée. Je présente entre autre dans ces perspectives les questions qui me viennent à leur suite.

Comment des flux de nutriments inorganiques reliant les écosystèmes jouerait alors sur leur stabilité et sur leur construction ?

La résolution de ces questions et la mise au jour des mécanismes sous-jacents amélioreront nos connaissances sur le fonctionnement des écosystèmes réels en poursuivant la construction d'une écologie plus intégrative et plus mécaniste.

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Résumé

Ce travail de thèse s'inscrit dans l'effort actuel de construction d'une écologie intégrative. J'y étudie les mécanismes d'interaction entre ressources abiotiques, réseaux trophiques et propriétés des écosystèmes, au moyen d'une expérience d'évolution, d'un modèle de méta-écosystème et d'un modèle bioénergétique d'assemblage d'écosystèmes. Les organismes modifient la disponibilité des ressources en les prélevant pour leur croissance. Inversement, la disponibilité des ressources influence la diversité et la composition en espèces du réseau trophique, en agissant comme force de sélection sur les traits d'acquisition des ressources (chap. 1, 5). Les propriétés de l'écosystème, telles que stabilité et productivité, dérivent des interactions entre la dynamique des ressources et celle du réseau trophique (chap. 2). Enfin, le fonctionnement de l'écosystème rétroagit sur les ressources abiotiques via le recyclage de la biomasse (chap. 2, 5). Ces processus interviennent lors de l'assemblage des réseaux trophiques et structurent le développement des écosystèmes (chap. 3-5). Dans cette thèse j'analyse ces mécanismes de rétroaction *biotique-abiotique* sur plusieurs échelles d'organisation, d'espace et de temps. Notamment, les modèles développés ici fournissent des outils novateurs pour étudier les mécanismes de construction des écosystèmes, en mettant en évidence les liens entre métabolisme des espèces, structure du réseau trophique et fonctionnement de l'écosystème, et leur variation au cours du temps. Ce travail ouvre de vastes perspectives de recherche en combinant les derniers progrès d'une écologie intégrative dans une conception mécaniste du développement des écosystèmes.

Mots-Clés : *biodiversité, développement des écosystèmes, assemblage des communautés, méta-écosystèmes, recyclage, nutriments inorganiques, modèle bioénergétique*

Abstract

This thesis participates to the current effort towards the construction of an integrative ecology. I study the feedback mechanisms between abiotic resources, food webs and ecosystem properties, through an evolution experiment, a model of metaecosystem, and a bioenergetic ecosystem assembly model. Organisms modify resource availability by consuming them for their growth. Conversely, resource availability influences the species diversity and composition of the food web, by acting as a selection pressure on traits for resource acquisition (chap. 1, 5). Ecosystem properties, such as stability and productivity, derive from the interactions between resource and food web dynamics (chap. 2). Finally, ecosystem functioning feeds back on abiotic resources through the recycling of biomass (chap. 2, 5). These processes occur during the food web assembly and drive the development of ecosystems (chap. 3-5). In this thesis I analyze these *biotic-abiotic* feedback mechanisms on several scales of organization, space and time. The models developed here provide innovative tools to study the mechanisms of ecosystem construction by pointing out the links between species metabolism, food web structure and ecosystem functioning, and their variation through time. This work opens wide research perspectives, as it combines the most recent progress of an integrative ecology into a mechanistic framework of ecosystem development.

Keywords: *biodiversity, ecosystem development, community assembly, metaecosystems, inorganic nutrients, recycling, bioenergetic model*